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Two new genera of gymnopoid/marasmioid euagarics

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Abstract—Two new genera, *Paramycetinis* and *Pseudomarasmius*, are placed phylogenetically within the /omphalotaceae among genera allied with *Gymnopus*. *Paramycetinis* comprises two Antipodal taxa related to *Mycetinis*. Both *Paramycetinis* species are characterized by luxuriant rhizomorphs, with basidiomata arising occasionally as side branches but also separately from rhizomorphs. *Pseudomarasmius* accommodates four new species plus four others previously placed in *Marasmius*. *Pseudomarasmius* encompasses significant basidiomatal variation, but nrLSU- and ITS-based phylogenies support its taxa in a monophyletic clade that occupies a position related to some *Rhodocollybia*. All *Pseudomarasmius* and *Paramycetinis* species are described (or redescribed) and illustrated. Both genera exhibit characters also found in other superficially similar lineages, making non-molecular based diagnoses of genera in the /gymnopus/marasmiellus clades difficult.

Key words— biogeography, clamp connections, morphological taxonomy

Introduction

For the last few decades, numerous, small, "white-spored" saprotrophic mushrooms have undergone a comprehensive reclassification. Especially edifying has been the introduction of molecule-based phylogenetic analyses at about the turn of the 21st century. New taxa have been identified at several nomenclatural ranks, from infraspecific (Aldrovandi & al. 2015; Petersen & Hughes 2016, 2017a,b) to class (Moncalvo & al. 2002, Matheny & al. 2006, Dentinger & al. 2016). In many cases, detailed morphological descriptions have accompanied molecular analyses (or the reverse), but "morphological taxa" are still being proposed without phylogenetic placement (Petersen &

Hughes 2016a, 2017; Retnowati 2018) when materials are too old or degraded to produce molecular data or the appropriate instrumentation is unavailable.

Desjardin (1989) summarized the classification and publication history of *Marasmius* and its segregation from *Gymnopus* (sensu Persoon 1801) or *Collybia* (sensu Fries 1821). The taxonomic history of *Gymnopus* (as *Collybia*) was outlined by Halling (1983). Subsequently, Antonín & al. (1997) discussed infrageneric taxonomy within *Marasmius* and *Gymnopus* (as *Collybia*), and Hughes & al. (2001) segregated *Gymnopus* (*G. fusipes* typus generis) from *Collybia* s.s. (*C. tuberosa* typus generis).

Owings & Desjardin (1997) apparently conducted the first research into the collybioid/marasmioid complexes using DNA sequences based on a more expanded thesis (Owings 1997; nrITS-based). Their work revealed that marasmioid fungi were not monophyletic but segregated into three lineages: present-day *Physalacriaceae*, *Omphalotaceae*, and *Marasmiaceae.* Moncalvo & al. (2000, 2002; LSU-based) essentially inferred the same. Mata & al. (2004; ITS- & LSU-based) showed that *Marasmiellus juniperinus* (typus generis) belonged in the omphalotoid complex, Wilson & Desjardin (2005) tied the morphological fragmentation of *Marasmius* to an nrLSU-based phylogeny and refined phylogenetic relationships of a wider array of organisms, and Mata & al. (2007; ITS-based) offered a more comprehensive phylogeny of /omphalotaceae, with emphasis on *Gymnopus.* The nomenclatural consequence of these works was circumscription of two major clades/families, *Marasmiaceae* and *Omphalotaceae*. A further consequence was more detailed fragmentation within these groups (Petersen & Hughes 2016a, 2017), in which *Gymnopus* as summarized by Mata & al. (2007) is clearly para- to polyphyletic with several related genera (*Rhodocollybia*, *Lentinula*, *Mycetinis*, *Connopus*) interspersed and *Gymnopanella* (Sandoval-Leiva & al. 2016) also associated. Three genera (*Lentinula*, *Rhodocollybia*, *Mycetinis*) are well-populated while two (*Connopus, Gymnopanella*) currently appear monotypic. If the concepts of Wilson & Desjardin (2005) are advanced to the present day, two large and complex clades contain traditional gymnopoid/marasmioid taxa: /Gymnopus incorporates *Gymnopus* sects. *Levipedes*, *Striipedes,* and *Impudici*, the traditional *Micromphale* (including sect. *Perforantia*), *Caripia*, and *Marasmius* sect. *Androsacei;* /Marasmiellus (including *M. juniperinus*, typus generis) includes *Gymnopus* sect. *Vestipedes* as well as *Marasmius* (*Marasmiellus*) *ramealis*, the type of *Collybiopsis* (J. Schröt.) Earle (Hughes & Petersen, ined.). /Marasmiellus) would appear to be a candidate for fractionation.

Oliveira & al. (2019) recognized their clade I (called "*Gymnopanella*") based on the taxon described by Sandoval-Leiva & al. (2016) and which included two provisional names that had appeared in phylogenies by Petersen & Hughes (2016). We regard those two provisional names as belonging in a separate generic unit, here proposed as *Paramycetinis*, based on its placement as sister to *Mycetinis*.

The intention of this paper is to propose two new genera, one comprising two new Antipodal species and the other accommodating several species. Figure 1 shows the relative placement of the new genera based on nrLSU-sequence resolution.

Materials & methods

Abbreviations: Pa = *Paramycetinis*; Ps = *Pseudomarasmius*; M = *Marasmius*; Ma = *Marasmiellus*; Mi = *Micromphale*; My = *Mycetinis*. Colors cited alphanumerically are from Kornerup & Wanscher (1967) or Munsell (1961), in quotation marks from Ridgway (1912), and special reference to Maerz & Paul (1950); BF = bright field microscopy; PhC = phase contrast microscopy (see also Petersen & Hughes 2017); TFB = Tennessee field-book number, assigned to fresh collections. In order to track information for collections from TENN, numbers are the last five digits of the fungal herbarium accession number (in MyCoPortal as TENN-F-0xxxxx); GSM (also GSMNP) = Great Smoky Mountains National Park, Tennessee/North Carolina. Percent similarity values within and between clades are given on the right.

Culture media reported to encourage rhizomorph production followed directions by Farnet & al. (1999). Two different whole wheat flours ("whole wheat flour" and "stone-ground whole wheat flour," both obtained locally) produced no difference in rhizomorph occurrence, number, or vigor. The term "textura" to describe the intricate crust formed by many marasmioid, mycetinoid, marasmielloid, and gymnopoid isolates in culture has been borrowed from Korf (1973), who used it to describe the excipular layer of apothecia.

Metrics of microstructures were calculated using a phase-contrast Olympus BX60 microscope fitted with phase contrast imagery and microphotographs were produced using an Olympus Qc color camera. Microscope mounts were usually in 3% KOH solution or Melzer's reagent.

Molecular methods for DNA extractions, PCR and Sanger sequencing of the nuclear ribosomal ITS and LSU regions follow Aldrovandi & al. (2015). PhyML phylogenetic analyses were performed in Geneious 11.0.3 (2017). Sequences have been deposited in GenBank (Table 1). Specimen data are available in MyCoPortal (2018). Nexis files containing nrLSU sequences and alignments were deposited in the Dryad Data Repository https://doi.org/10.5061/dryad.4081h). ITS sequence %-similarity is the average of all paired sequences computed by Geneious 11.0.3 (2017) as "percent identity".

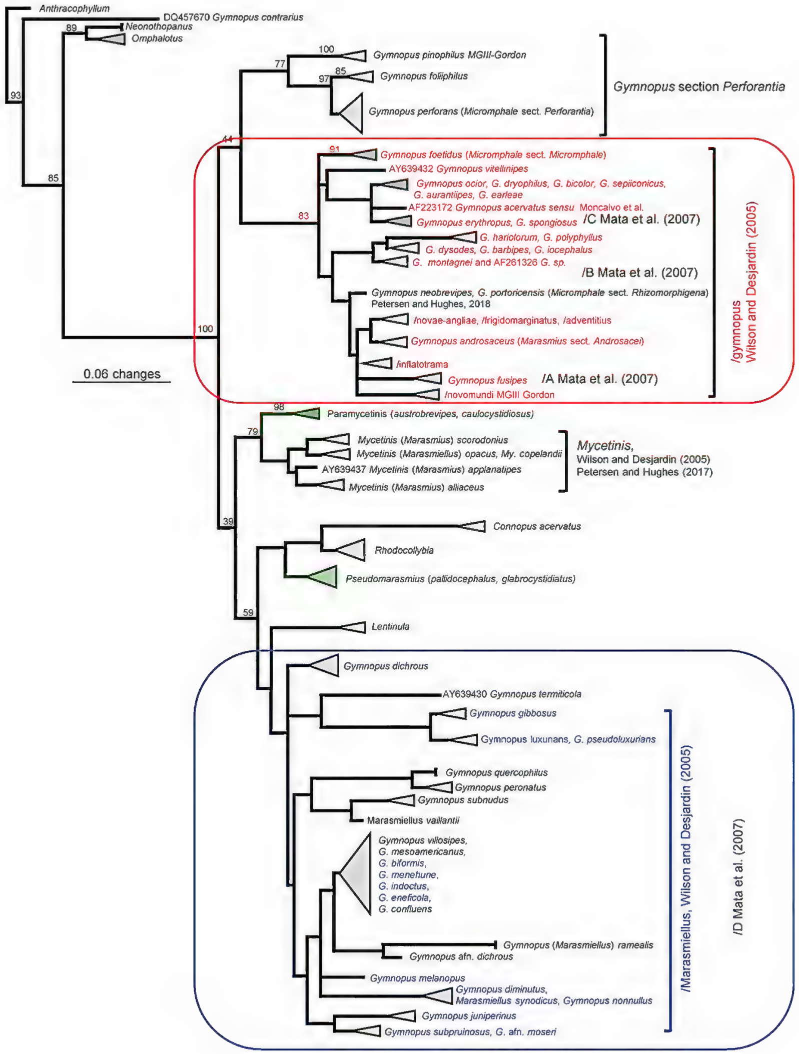
Anthracophyllum
DQ457670 Gymnopus contrarius
89
Neonothopanus
Omphalotus
93
85
100
Gymnopus pinophilus MGIII-Gordon
77
85
Gymnopus foliiphilus
97
Gymnopus perforans (Micromphale sect. Perforantia)
Gymnopus section Perforantia
44
91
Gymnopus foetidus (Micromphale sect. Micromphale)
AY639432 Gymnopus vitellinipes
Gymnopus ocior, G. dryophilus, G. bicolor, G. sepiiconicus,
G. aurantiipes, G. earleae
AF223172 Gymnopus acervatus sensu Moncalvo et al.
83
Gymnopus erythropus, G. spongiosus
/C Mata et al. (2007)
G. hariolorum, G. polyphyllus
G. dysodes, G. barbipes, G. iocephalus
G. montagnei and AF261326 G. sp.
/B Mata et al. (2007)
Gymnopus neobrevipes, G. portoricensis (Micromphale sect. Rhizomorphigena)
Petersen and Hughes, 2018
/novae-angliae, /frigidomarginatus, /adventitius
Gymnopus androsaceus (Marasmius sect. Androsacei)
100
/inflatotrama
0.06 changes
Gymnopus fusipes
/A Mata et al. (2007)
/novomundi MGIII Gordon
/gymnopus
Wilson and Desjardin (2005)
98
Paramycetinis (austrobrevipes, caulocystidiosus)
79
Mycetinis (Marasmius) scorodonius
Mycetinis (Marasmiellus) opacus, My. copelandii
AY639437 Mycetinis (Marasmius) applanatipes
Mycetinis (Marasmius) alliaceus
Mycetinis,
Wilson and Desjardin (2005)
Petersen and Hughes (2017)
39
Connopus acervatus
Rhodocollybia
Pseudomarasmius (pallidocephalus, glabrocystidiatus)
59
Lentinula
Gymnopus dichrous
AY639430 Gymnopus termiticola
Gymnopus gibbosus
Gymnopus luxunans, G. pseudoluxurians
Gymnopus quercophilus
Gymnopus peronatus
Gymnopus subnudus
Marasmiellus vaillantii
Gymnopus villosipes,
G. mesoamericanus,
G. biformis,
G. menehune,
G. indoctus,
G. eneficola,
G. confluens
Gymnopus (Marasmiellus) ramealis
Gymnopus afn. dichrous
Gymnopus melanopus
Gymnopus diminutus,
Marasmiellus synodicus, Gymnopus nonnullus
Gymnopus juniperinus
Gymnopus subpruinosus, G. afn. moseri
/Marasmiellus, Wilson and Desjardin (2005)
/D Mata et al. (2007)

Fig. 1. PhyML analysis of 191 nrLSU sequences within the *Omphalotaceae* using 100 bootstrap replicates. Clades were collapsed to better show broad relationships. Species names in blue represent /marasmiellus (Wilson & Desjardin 2005). Species names bordered in red represent /gymnopus (Wilson & Desjardin 2005). The major clades reported in Mata & al. (2007) are bordered in blue. The genera *Paramycetinis* and *Pseudomarasmius* are in green.

Table 1. Collections used in phylogenetic analyses

Name	GenBank #	Herbarium #	Field #	Locality
[Fig. 2—*Gymnopus, Paramycetinis, Mycetinis*]				
Gymnopus perforans	KY026675	TENN-F-61587	TFB13119	Canada, Quebec
	KY026719	TENN-F-69059	TFB14395	Canada, New Brunswick
G. foliiphilus	KY026703	TENN-F-68145	TFB14291	USA, Mississippi
G. sequoiae	KY026741	TENN-F-69325	TFB14620	USA, California
Paramycetinis austrobrevipes	KY026622	TENN-F-50135	TFB4033	Australia
	KY026637	TENN-F-53149	TFB3591	Australia
	KY026638	TENN-F-53181	TFB3585	Australia
P. caulocystidiatus	KY026642	TENN-F-53683	TFB7572	New Zealand
	KY026643	TENN-F-53721	TFB7588	New Zealand
	KY026644	TENN-F-53725	TFB7589	New Zealand
	KY026645	TENN-F-54050	TFB7148	New Zealand
Mycetinis alliaceus	AY635776	TENN-F-55620	TFB8960	Russia
	DQ450004	TENN-F-55555	TFB8935	Russia
	KY696752	TENN-F-55630	TFB8970	Russia
	KY696765	TENN-F-67899	TFB14149	Germany
	KY696766	TENN-F-67911	TFB14161	Germany
	KY696770	TENN-F-69243	TFB14548	Slovakia
	KY696771	TENN-F-69244	TFB14549	Slovakia
M. applanatipes	KY696775	SFSU DED6628	—	USA, California
M. copelandii	KY696750	TENN-F-55408	TFB8084h1	USA, California
	KY696751	TENN-F-55408	TFB8084h2	USA, California
M. kallioneus	KX958397	GB-0150513	—	Norway
M. opacus	KY696758	TENN-F-60016	TFB11787	USA, Tennessee, GSMNP
	KY696767	TENN-F-69190	TFB14499	Mississippi
	KY696768	TENN-F-69200	TFB11490h1	Mississippi
	KY696769	TENN-F-69200	TFB11490h2	Mississippi
M. querceus	KY696785	UPS F740422	—	Sweden
M. salalis	KX752265	DAOM175251	—	Canada, BC, Vancouver Isl.
M. scorodonius	DQ450006	TENN-F-50346	TFB4749	Switzerland

Name	GenBank #	Herbarium #	Field #	Locality
	KY696725	TENN-F-50343	TFB4746	Switzerland
	KY696726	TENN-F-50352	TFB4755	Switzerland
	KY696727	TENN-F-50369	TFB4772	Switzerland
	KY696728	TENN-F-50377	TFB4780	Switzerland
	KY696729	TENN-F-50447	TFB4372	Mexico
	KY696730	TENN-F-50515	TFB3778	Sweden
	KY696731	TENN-F-50522	TFB3785	Sweden
	KY696732	TENN-F-50533	TFB3796	Sweden
	KY696733	TENN-F-50689	TFB3701	USA, North Carolina
	KY696734	TENN-F-50696	TFB3708	USA, TN GSMNP
	KY696735	TENN-F-50763	TFB3644	USA, TN GSMNP
	KY696736	TENN-F-50809	TFB3690H1	USA, TN GSMNP
	KY696737	TENN-F-50809	TFB3690H2	USA, TN GSMNP
	KY696738	TENN-F-51233	TFB4915	USA, North Carolina
	KY696739	TENN-F-51442	TFB5031	Canada, Nova Scotia
	KY696740	TENN-F-53465	TFB5014	Canada, Nova Scotia
	KY696741	TENN-F-53466	TFB4969	USA, New York
	KY696742	TENN-F-53467	TFB5025	Canada, Nova Scotia
	KY696743	TENN-F-53468	TFB5038	Canada, Nova Scotia
	KY696744	TENN-F-53469	TFB4989	USA, Maine
	KY696745	TENN-F-53470	TFB5046	USA, North Carolina
	KY696746	TENN-F-53471	TFB4939	USA, New York
	KY696747	TENN-F-53472	TFB5067	USA, North Carolina
	KY696748	TENN-F-53474	TFB5005	USA, Maine
	KY696749	TENN-F-53568	TFB7261	Sweden
	KY696753	TENN-F-57663	TFB2782	USA, Georgia
	KY696754	TENN-F-58260	TFB10400	Russia, Western
	KY696757	TENN-F-59615	TFB11652	Russia
	KY696786	WTU19061H1	—	USA, Washington
	KY696787	WTU19061H2	—	USA, Washington

Name	GenBank #	Herbarium #	Field #	Locality
[Fig. 15—*Gymnopus, Marasmius, Pseudomarasmius,* cf. *Rhodocollybia,* etc.]				
Gymnopus glabrocystidiatus **(T)**	NR152899	BRNM718676	—	Korea
	KF251072	KFRI1935	—	Korea
Marasmius sp.	KR673444	KA12-0382	—	South Korea
Pseudomarasmius quercophiloides	MK268235	TENN-F-49177	TFB3162	China, Yunnan
Ps. efibulatus	MK268234	TENN-F-56187	TFB7070	New Zealand, South Island
	MK268236	JAC10695	—	New Zealand
Ps. patagonianus	KY352649	TENN-F-54424	TFB7364	Chile
Ps. nidus-avis	KY026646	TENN-F-54912	TFB9087	USA, Louisiana
	KY026723	TENN-F-69189	TFB14498	USA, Mississippi
	KY026732	TENN-F-69310	TFB14607	USA, Alabama
	KY026733	DPL11763	—	USA, Texas
	KY026753	Rhizomorph culture	TFB14606	USA, Mississippi
	MK020094	—	MES883	USA, Florida
	MK268237	FLAS-F-62667	MES1477	USA, Florida
	MK268238	FLAS-F-62668	MES3139	USA, Florida
	MH016872	FLAS-F-60891	—	USA, Florida
Ps. pallidocephalus	KY026635	TENN-F-52401	5610 culture	USA, Idaho
	FJ596762	TENN-F-59896	TFB11778h2	USA, TN GSMNP
	FJ596763	TENN-F-59896	TFB11778h1	USA, TN GSMNP
	KY026636	TENN-F-52427	TFB5698	USA, Washington
	KY026684	TENN-F-65829	TFB13933h1	USA, New York
	KY026685	TENN-F-65829	TFB13933h2	USA, New York
	KY026691	TENN-F-66344	SAT11-179-05	USA, TN GSMNP
	KY026746	no specimen	5015 culture	Canada, Nova Scotia
Rhodocollybia	FJ475743	soil sample	—	Sweden
aff.	KC966049	soil sample	—	Alaska
R. sp.	AY313287	TENN-F-58798	TFB10712	Greenland
Tricholomataceae	LCO14889	no specimen	8PBL11	Japan, Nagano
—	JN890248	soil sample	—	Guyana
—	JN890219	soil sample	—	Guyana
—	JN890249	soil sample	—	Guyana

Paramycetinis

The nrLSU sequence analysis places *Paramycetinis* within a moderately supported clade that includes *Mycetinis* (Fig. 1). A PhyML analysis of *Mycetinis* and *Paramycetinis* nrITS sequences (Fig. 2) places *Paramycetinis* as sister to a clade containing several *Mycetinis* species. The average base pair identity between *Paramycetinis* and *Mycetinis* is 91.72%.

Only sparse literature on marasmioid fungi from Australia (Fuhrer 1985), South Australia (Cleland 1934, Grgurinovic 1997), and Tasmania (Eygelsheim 1981, Fuhrer & Robinson 1972) preceded introduction of molecular phylogenetic analyses. Those publications grouped collections of small marasmioid basidiomata as "*Marasmius crinis-equi*" or "horse-hair fungi" according to the presence of obvious rhizomorphs when, in fact, several discrete taxa qualify under this superficial diagnosis and await formal proposals. More recently, Desjardin & Horak (1997) revisited earlier work by Stevenson (1964) and Horak (Horak 1971a,b) to revise numerous marasmioid fungi from Papua New Guinea, New Caledonia, and New Zealand, and Desjardin & al. (2000) summarized *Marasmius* for parts of Indonesia.

Even less literature dealt with *Micromphale* (here understood as *Gymnopus* sect. *Micromphale*) on the Australia/New Zealand landmasses [but see Cooper & Leonard (2013) on micromphalioid *Gymnopus* taxa]. To our knowledge, only Grgurinovic (1997) has dealt with species of sect. *Perforantia* (*Agaricus perforans*, typus sectionis); she placed *Micromphale australiense, M. rugosum*, and *M. villosipes* (all from South Australia) in *Micromphale* based solely on morphological characters.

Owings & Desjardin (1997) first identified three infrageneric phylogenetic clusters accommodating *Marasmius* taxa; subsequent phylogenetic studies refined this early finding. In nrLSU sequence analyses of marasmioid and gymnopoid fungi, Wilson & Desjardin (2005) identified a clade including taxa previously segregated into the morphogenus *Mycetinis* Earle (1909; *Agaricus alliaceus,* typus generis). This clade was also resolved by Mata & al. (2004, 2007) but not nomenclaturally separated from *Gymnopus*, which they accepted in a very broad sense. Petersen & Hughes (2016), who also showed a /mycetinis clade in their overall nrLSU phylogeny of *Gymnopus* and associated genera, found that /mycetinis comprised three subclades, of which the sister subclade to *Mycetinis* contained sequences of two taxa known only from Tasmania and New Zealand. This small subclade, sister to /mycetinis, is taken up here as *Paramycetinis*.

/Mycetinis is presently accepted as inclusive of traditionally disparate morphological taxa. From its re-disclosure by Wilson & Desjardin (2005; LSU-based), *My. alliaceus* and *My. scorodonius* were joined by *Marasmiellus opacus*, so Wilson & Desjardin (2005) furnished a discussion of morphological characters justifying inclusion of *Ma. opacus* in /mycetinis and proposed appropriate transfers. Likewise, Mata & al. (2007; ITS-based) placed *Ma. candidus* in the same clade although Wilson & Desjardin (2005) had placed it in /tetrapyrgos, an adjoining clade. At genus rank, *Mycetinis* has been accepted by Antonín & Noordeloos (2010) and lately surveyed by Petersen & Hughes (2017b). One ITS-based PhyML phylogeny (Fig. 2) shows the relationship of *Paramycetinis* to *Mycetinis*.

Oliveira & al. (2019) recognized a small clade (their clade I) called "*Gymnopanella*," based on the taxon described by Sandoval-Leiva & al. (2016). Their clade I included two provisional names that appeared in phylogenies by Petersen & Hughes (2016). We consider the two provisional names to belong in a separate generic unit, here proposed as *Paramycetinis*.

Paramycetinis R.H. Petersen, **gen. nov.**

IF 555792

Basidiomata diminutive, associated with dominant black rhizomorphs; a monophyletic clade.

Type species: *Paramycetinis austrobrevipes* R.H. Petersen

Etymology: reflecting the sister phylogenetic relationship to *Mycetinis*.

Basidiomata combining characters of *Gymnopus* sect. *Micromphale* subsect. *Perforantia*, *Gymnopus* sect. *Androsacei*, and *Marasmius* sect. *Sicci*, minute to small, arising as rhizomorph branches or separate from rhizomorphs. Pileus small (3–15 mm broad), some shade of brown or vinaceous brown, sometimes sulcate-striate, smooth or minutely pruinose; pileus trama thin, pliant. Lamellae adnexed to adnate, sometimes attached to an adherent pseudocollarium, close to subdistant, from ridge-like to well-developed, usually with lamellulae in 1–2 ranks, off-white to dull vinaceous gray. Stipe capillary, ≤3 mm broad, terete, more or less equal, solid to stuffed, glabrous-shining to minutely velutinous, brown to brown-black, especially downward, insititious (when not a rhizomorph branch). Rhizomorphs common, ranging from very slender to stout, sometimes dominant and forming loose nets, usually black. Pileipellis commonly involved in slime as a matrix and/or as gelatinizing hyphal walls, usually including diverticulate hyphae and broom cell-like hyphal termini. Pleurocystidia ubiquitous, narrowly to broadly fusiform; contents

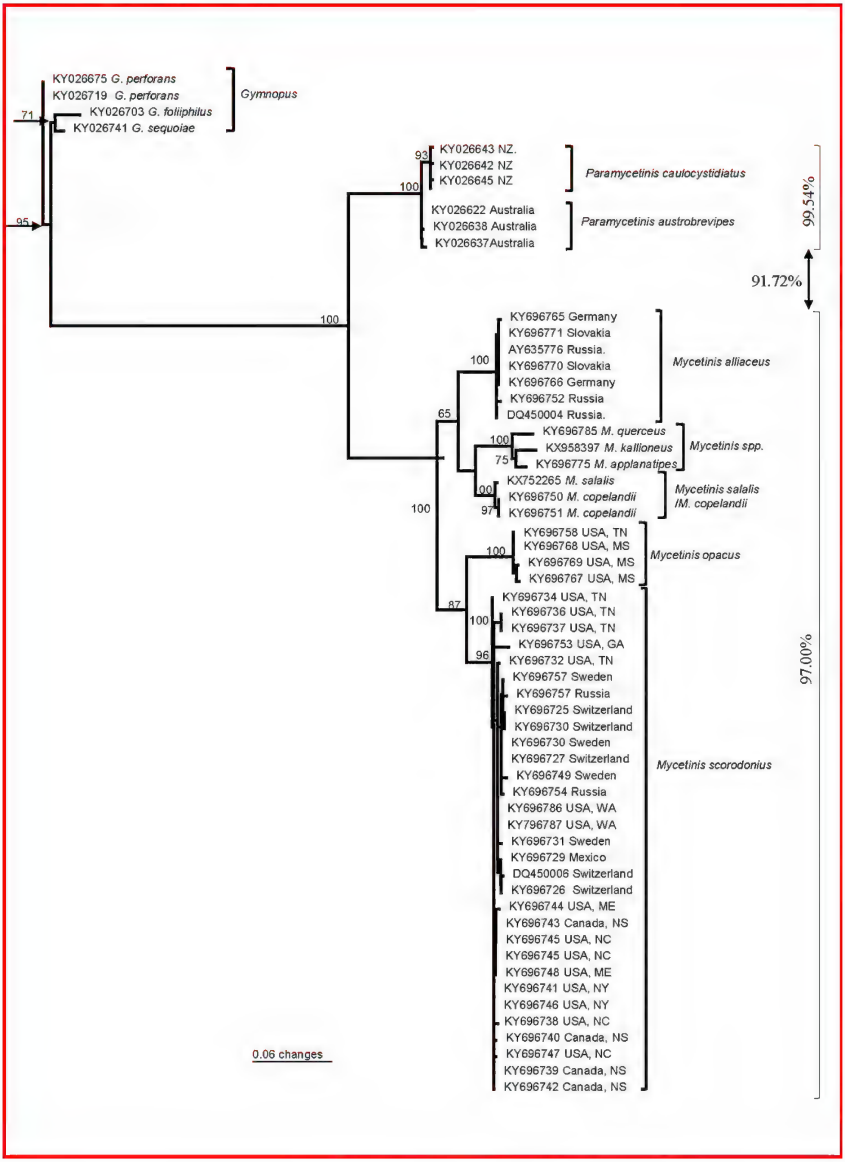

FIG. 2. Maximum likelihood analysis of combined ribosomal RNA ITS and LSU sequences. Bootstrap values are given to the left of the supported node. Numbers are GenBank accession numbers (See TABLE 1). For collections from the United States and Canada, the state or province postal code is given. Percent similarity values within and between clades are given on the right.

more or less homogeneous, occasionally vaguely partitioned. BASIDIA clavate, 4-sterigmate. BASIDIOSPORES thin-walled, smooth, inamyloid, white or off-white in deposits. CHEILOCYSTIDIA present, arbuscular (stalked, branched) or broadly clavate, with or without diverticula. STIPE MEDULLARY HYPHAE strictly parallel, usually involved in a slime matrix. CAULOCYSTIDIA present or absent, when present gregarious to scattered (not a dense turf), setoid. CLAMP CONNECTIONS present. Molecular analysis resolving a monophyletic clade associated with *Mycetinis*.

Key to taxa of *Paramycetinis*

1. Rhizomorphs stout (>1 mm diam), forming loose nets; basidiomata arising from or separate from rhizomorphs; cheilocystidia clavate with clusters of apical setulae (Tasmania) .... *Pa. austrobrevipes*

1. Rhizomorphs slender (<1 mm diam), extensive; basidiomata arising separate from rhizomorphs; cheilocystidia clavate, without diverticula; fruiting on dead leaves and twigs of *Nothofagus* (New Zealand) .... *Pa. caulocystidiatus*

Paramycetinis austrobrevipes R.H. Petersen, **sp. nov.** FIGS 3–8

IF 555793

Differs from *Paramycetinis caulocystidiatus* by its broader rhizomorphs that form loose nets, by its basidiomata that arise as rhizomorph branches and/or from woody substrate, and by its broom cell-like cheilocystidia.

TYPE: Australia, Tasmania, Gordon-Pedder National Heritage Area, Rainforest Nature Walk vicinity, 8.VI.1991, coll. RHP & KWH, TFB 4033 (**Holotype** TENN-F-050135).

ETYMOLOGY: referring to micromorphological similarities to *Gymnopus neobrevipes*.

BASIDIOMATA (FIG. 3) marasmioid, diminutive, arising as branches from rhizomorphs and/or directly from woody substrate. PILEUS 2–12 mm broad, convex to shallowly conical, sometimes abruptly or broadly umbonate and even then abruptly umbilicate, deeply sulcate-striate to non-striate, matte, at high magnification (50×) telltale wispy white hairs can be seen in the sulcate depressions; disc (including umbo) 5F6 ("Prout's brown"), 6E3 ("hair brown"), 9D3 ("benzo brown"), 7C4 ("wood brown"), 6E4 ("fuscous"), 7C6 ("Mikado brown") to 9C3 ("cinnamon drab"); limb 6C5 ("sayal brown"), 6B5 ("cinnamon"), 17B2 ("light drab"), 7B2 ("tilleul buff"), to 9B2 ("vinaceous buff"), 8D5 ("army brown"), 9C3 ("cinnamon drab"), 9B3 ("light cinnamon drab") to 7C5 ("fawn color"); margin 6A3 ("pinkish buff") to 4A3 ("cartridge buff"). LAMELLAE adnexed, subdistant (total lamellae 20–24), about 1 mm broad, thickish, without anastomoses, 7B2 ("tilleul buff"), 9B2 ("vinaceous buff"), 6B4 ("cinnamon buff") to 6A3 ("pinkish buff"), not marginate; dried lamellar trama dark brown and glassy, as though gelatinized. Stipe 18–85 × 0.8–1.2 mm, terete, stuffed (not hollow), appearing glabrous–shining but minutely pruinose at least upward and downward (35×), black to abruptly 6C5 ("sayal brown"), 6B3 ("cinnamon buff") or mahogany at very apex (not concolorous with lamellae), downward totally black; medullary portion cloud gray, cortical layer thin, nearly black (40×); insertion non-insititious; vesture sparse, pallid, near 7B2 ("tilleul buff"). Rhizomorphs >1 mm broad, gradually tapering to 0.2–0.5 mm distally, terete or somewhat compressed, extensive to almost absent, often forming a rudimentary net. Odor negligible; taste negligible or weak of garlic; consistency tough then mealy.

Habitat & phenology: *Nothofagus* wood (and then densely gregarious) and twigs, at or near forest floor, *Arthrotaxis* dead branchlets; to this time, May–June.

Pileipellis constructed of the following: 1) slender hyphae 2–3.5 µm diam, thick-walled (wall <0.5 µm thick), sparsely encrusted (Fig. 4a) with ornamentation appearing as flakes adhered to outer hyphae wall; 2) slender hyphae 1.5–3 µm diam, firm-walled with slender, sometimes awl-shaped diverticula (Fig. 4b, 5a–d), obscurely clamped, forming a indiscrete layer in a mucoid matrix (i.e. significant debris including bacteria and collapsed spores, PhC); 3) slender, coralloid hyphal termini (Fig. 5e,f); 4) thicker hyphae 4–12 µm diam, refringent (PhC), infrequently branched, meandering to appear a bit like lattice, thick or gelatinized–walled (wall <2.5 µm thick), with outer profile smooth and clear but inner wall contour irregular, obscurely clamped; termini occasionally more or less erect as "pileal hairs." Pleurocystidia (Figs 6b, 7a–c) common, 26–33 × 5–9 µm, fusiform to mucronate, conspicuously clamped, usually with partitioned contents. Basidia 23–28 × 6–9 µm, clavate, 4-sterigmate (sterigmata <6 µm long, somewhat bowed, stout), obscurely clamped; contents homogeneous. Basidiospores (Fig. 6a) 6–9 × 3.5–4.5 (–5) µm ($Q = 1.502.43$; $Q^m = 1.92$; $L^m = 7.47$ µm), more or less pip-shaped but often tapered slightly proximally (that is, perhaps marasmioid), smooth, thin-walled, inamyloid; contents homogeneous. Cheilocystidia (Figs 6d, 7e–h) locally common to scattered among basidia, 17–32(–40) × 5–12 µm, clavate to ventricose-rostrate, obscurely clamped, thin-walled below, firm-walled above, surmounted by a corona of extremely complex, vermiform to slender-digitate, refringent (PhC) diverticula; diverticula <7 × 0.71 µm, gnarled, often branched. Stipe medullary hyphae hyaline, 2–5.5 µm diam, firm- to thick-walled, seldom but conspicuously clamped; cortical

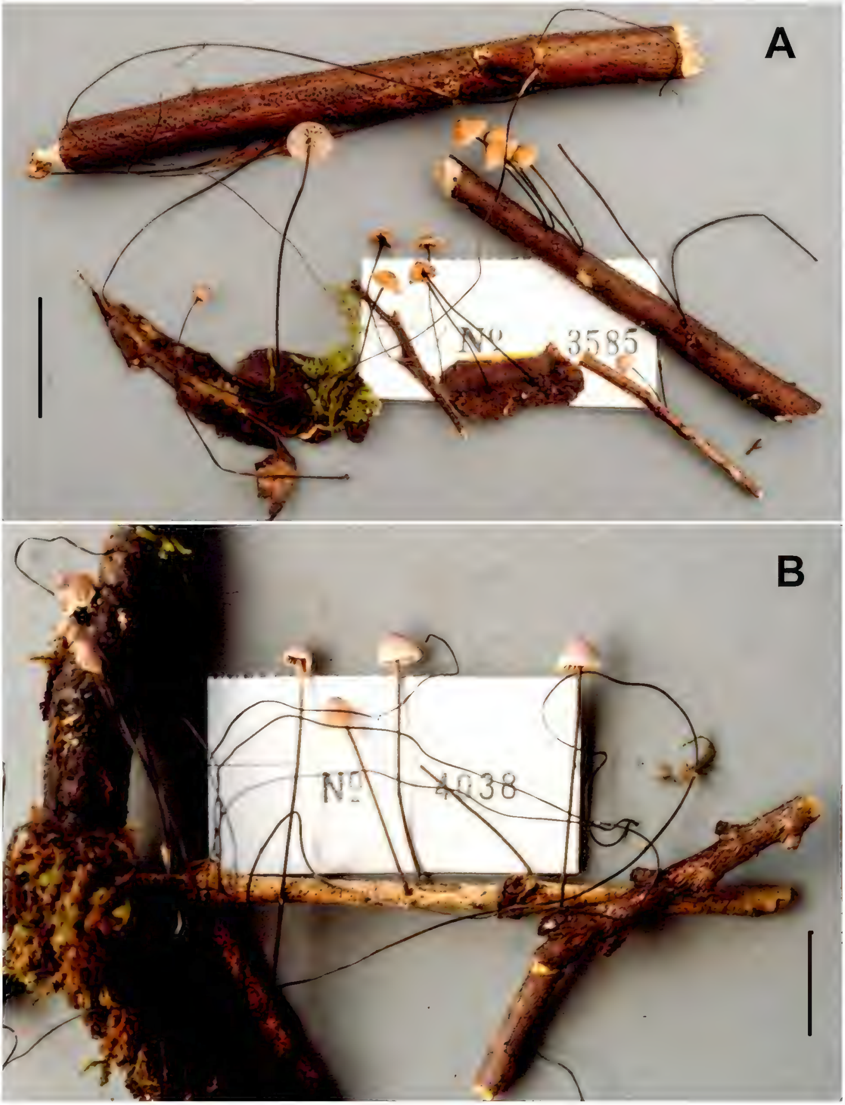

Fig. 3. *Paramycetinis austrobrevipes*.
Habit. A. (TENN 53181). B. (TENN-F- 050212). Scale bars: 20 mm.

HYPHAE adherent, 3–7 µm diam, yellow singly, dark ochraceous brown and refringent in mass (PhC), involved in a thin film of mucus, with side branches ranging from simple lobes to caulocystidia. CAULOCYSTIDIA (Fig. 8)

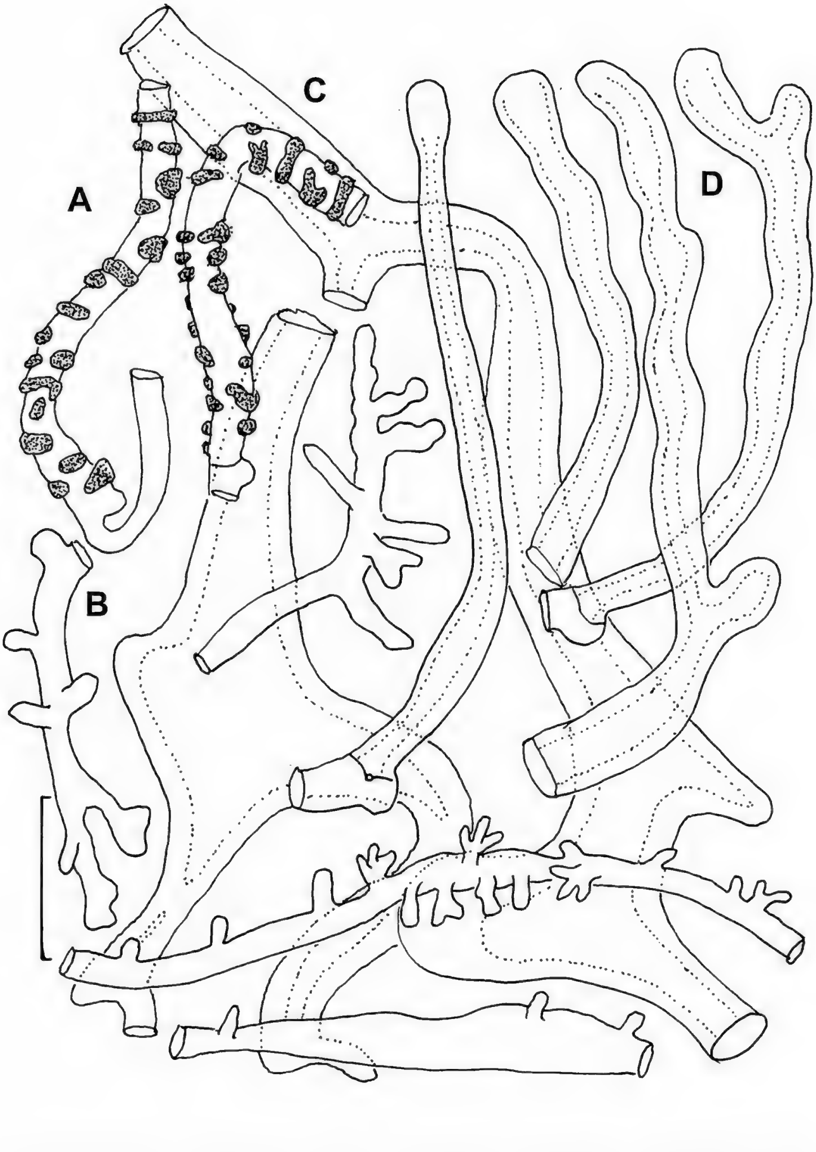

FIG. 4. *Paramycetinis austrobrevipes*. Structures of pileipellis. A. Encrusted hyphae (TENN 50119). B. Diverticulate hyphae (TENN-F-050135). C. Thick-walled lattice hyphae (TENN-F-050135). D. Pileal hairs (TENN-F-050119. Scale bars: 20 µm.

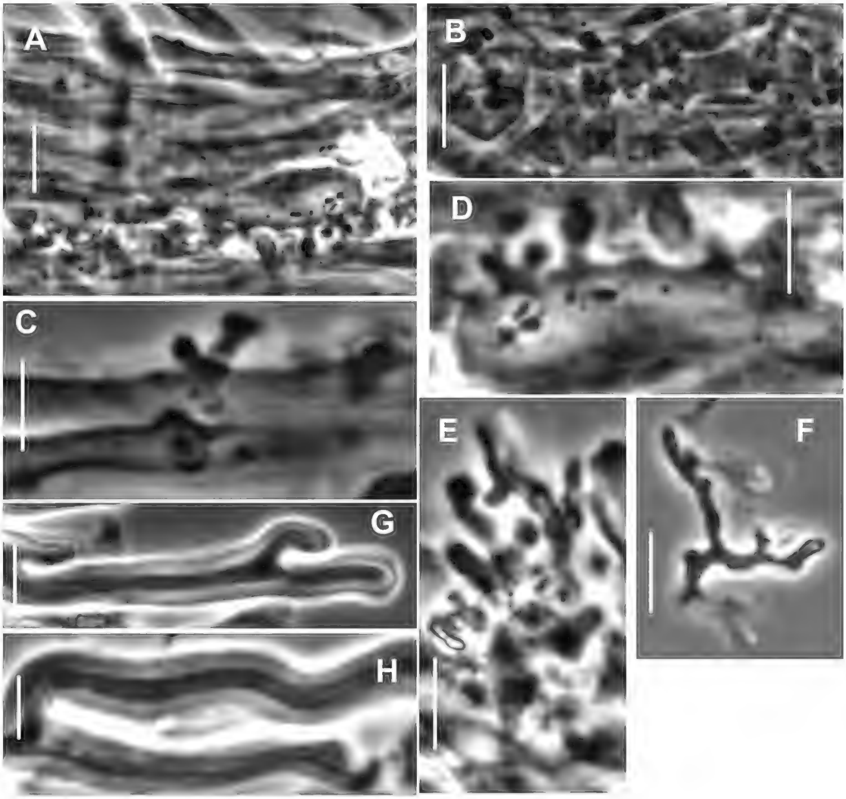

FIG. 5. *Paramycetinis austrobrevipes* (TENN-F-050135). Pileipellis elements. A. Layer of diverticulate hyphae as embedded within pileipellis. B. Layer of diverticulate hyphae. C,D. Individual diverticulate hyphae. E, F. Broom cell-like hyphal termini. G,H. Hyphae with gelatinized walls. Scale bars: 10 µm.

scattered, <105 × 46 µm (at widest point, narrowing to 3–3.5 µm diam at base, 2–3 µm diam at apex), gregarious but more or less evenly distributed, usually single, rarely in pairs, as side branches of stipe surface hyphae, apparently near the terminus of such hyphae (and therefore appearing as though from an asymmetrical origin, yellow and refringent (PhC), so refringent that wall thickness is hardly discernible (when wall seems to be discernible, 1–1.5 µm thick), narrowly rounded apically and apparently without adherent debris, dextrinoid (Melzer's reagent + PhC) or brown (Melzer's reagent + BF), not internally septate.

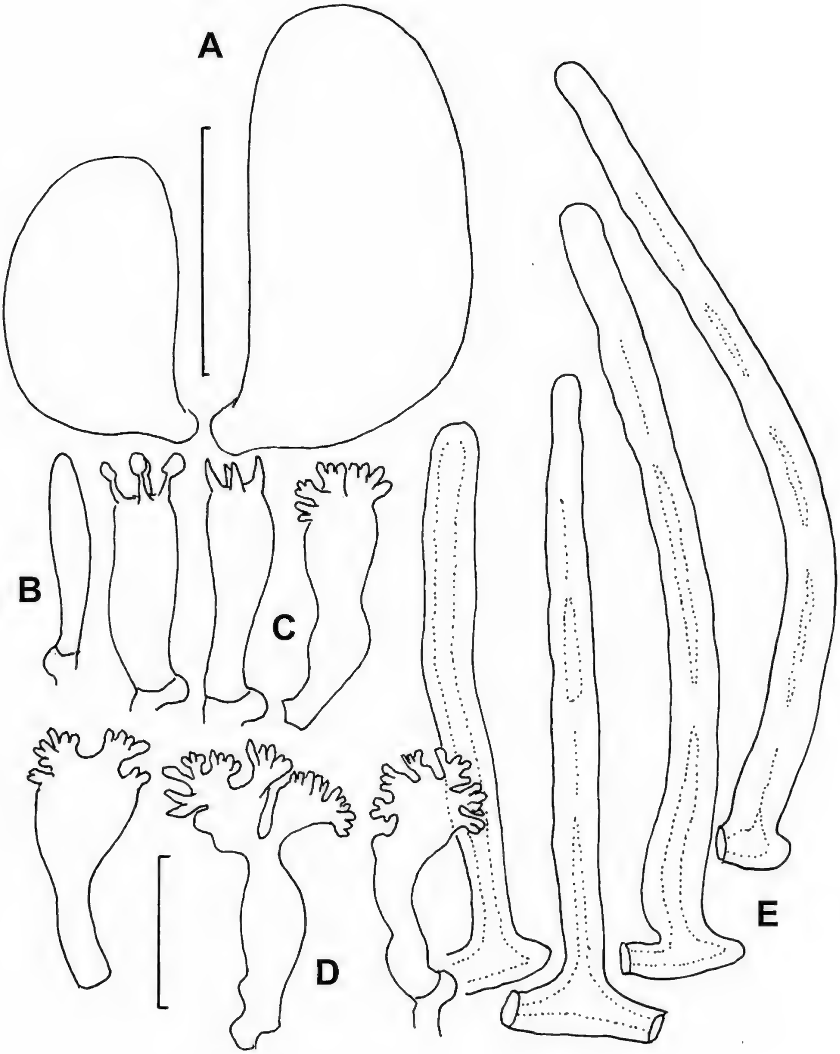

Fig. 6. *Paramycetinis austrobrevipes* (TENN-F-050135).
A. Basidiospores. B. Pleurocystidium. C. Basidia. D. Cheilocystidia. E. Caulocystidia.
Scale bars: A = 5 µm; B–D = 20 µm.

Commentary: Pileus shape in *Pa. austrobrevipes* varies from convex with an abrupt, distinct umbo to a gradual and shallow umbo to no evidence of an

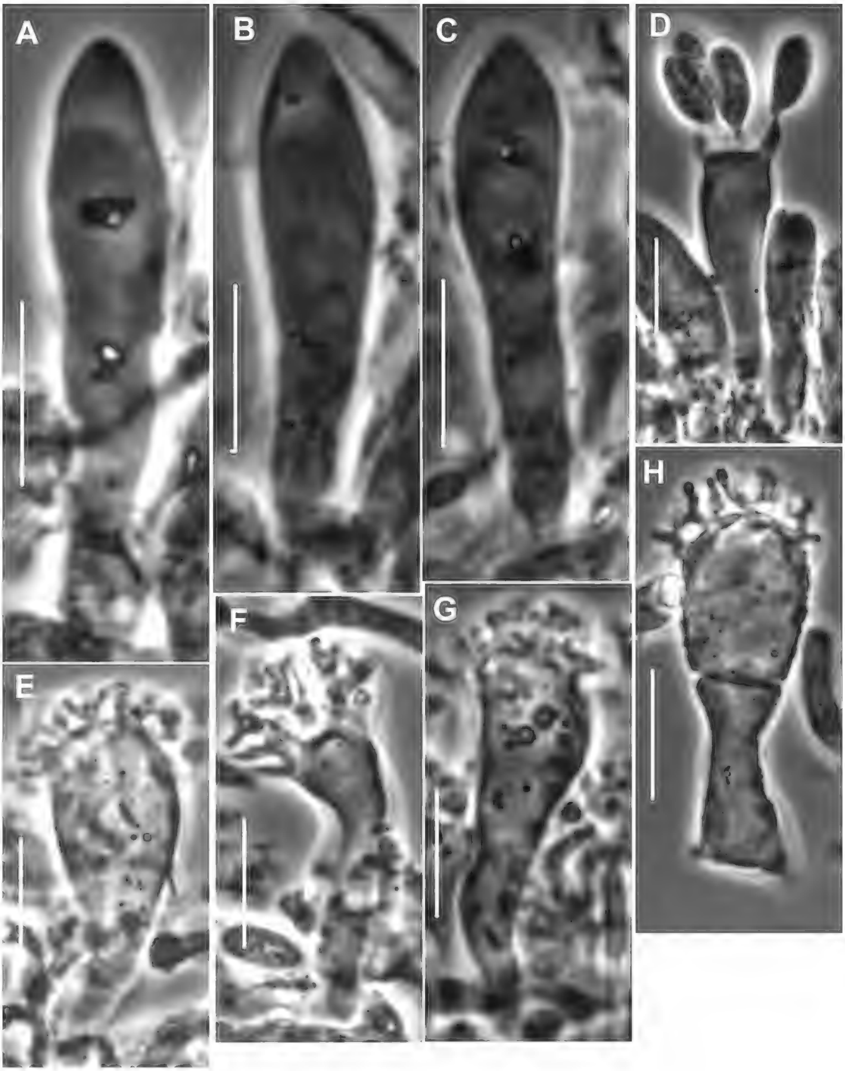

Fig. 7. *Paramycetinis austrobrevipes* (TENN-F-050135).
A–C. Pleurocystidia. D. Basidium. E–H. Cheilocystidia. Scale bars: 10 µm.

umbo. In all cases, the disc (with or without umbo) is significantly darker than the limb.

The pileus micromorphology of *Pa. austrobrevipes* approaches that of the North American *Marasmius brevipes* [≡ *Gymnopus neobrevipes* R.H. Petersen &

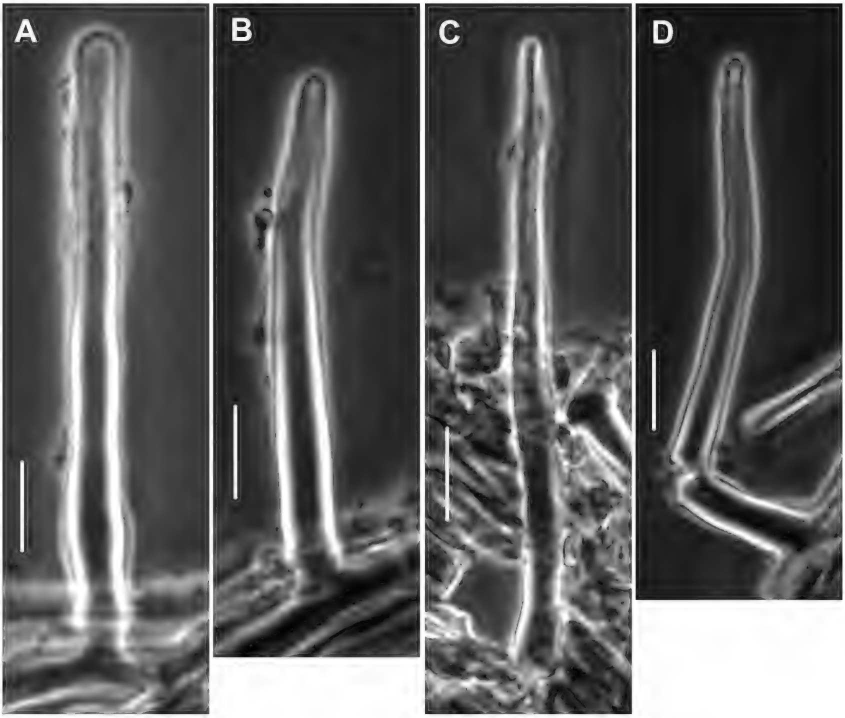

Fig. 8. *Paramycetinis austrobrevipes* (TENN-F-050135).
Caulocystidia. Scale bars: 10 µm.

Hughes 2019)]. Basidiomata of both species arise on woody substrate (usually twigs with thin bark intact or occasionally as branches from an extensive rhizomorph net), but *G. neobrevipes* basidiomata are small and thumb tack-shaped while those of *Pa. austrobrevipes* are tall and mycenoid. Pileus colors are similar but also characteristic of several taxa in *Gymnopus* sect. *Androsacei*. Rhizomorphs and stipes are black, although stipe in *G. neobrevipes* is glabrous throughout its length. There is no record of a weak or latent taste of garlic for *G. neobrevipes*. Comparison of notes and drawings of *G. neobrevipes* specimens indicate that it also has a gelatinizing pileipellis, but with a more demonstrable "*ramealis*-structure." *Gymnopus neobrevipes* basidiomata also occur independently from rhizomorphs as well as branches from rhizomorphs, and its rhizomorphs are also thick and form an aerial network as well as on the substrate surface. Despite these similarities, molecular evidence shows *Pa. austrobrevipes* and *G. neobrevipes* to be only distantly related (see Fig. 1).

The surviving culture of TENN-F-053181 (TFB 3585) formed considerable aerial mycelium and what appears to be resupinate rhizomorphs against the side of the MEA-slanted storage test tube. This is different from other cultures of the same putative species but identical to a culture of TFB 3966, of which voucher basidiomata are no longer extant.

Collections of *Pa. austrobrevipes* may be mistaken in the field for *M. crinis-equi*. The latter can be distinguished in the field by collariate lamellae, significantly smaller basidiomata with short, curved stipes and typical hymeniform pileipellis and cheilocystidia. Grgurinovic (1997) cited collections of *M. crinis-equi* from New South Wales and South Australia, and Pegler (1977) furnished a much wider range for the species.

Close inspection of rhizomorph surfaces shows that when rhizomorphs branch, whether to produce a basidiome or a sterile branch, there is often a rupture of the parent rhizomorph cortex—splitting the cortex and revealing the medulla. This rupture is sparsely covered by a brown mycelium, which also covers the basal portion (<50 µm) of the new branch. Whether sterile or fertile, the new branch is also vestured with caulocystidia, which peter out in less than a millimeter distally, leaving the greater portion of the rhizomorph branch (or stipe) subglabrous.

On whole wheat flour agar (Farnett & al. 1999), cultures of *Pa. austrobrevipes* produced chiefly submerged mycelium, no textura intricata, and no rhizomorphs. TFB 3591 (TENN-F-053146) produced a minutely granular white mycelial mat with ill-defined margins.

Text and illustrations of *Paramycetinis* species were generously pre-reviewed by Australian and New Zealand mycologists in order to avoid nomenclatural duplication of any taxon already described. While no present-day match was suggested (but see below), five historical names under *Marasmius* were pointed out, as follows:

Marasmius eucalypti Berk., in Hooker, Fl. Tasman. 2: 249, 1859 [“1860”].

Pegler (1965: 331) examined the type specimen. While a basidioma is illustrated as arising as a side branch of a rhizomorph, pileipellis was described as “hymeniform, composed of diverticulate elements similar to the cheilocystidia.” Thick-walled caulocystidia are described and illustrated. All of this indicates identification as a *Marasmius*, probably *M.* sect. *Sicci*.

Marasmius meloniformis Berk., in Hooker, Fl. Tasman. 2: 249, 1859 [“1860”].

Pegler’s (1965: 339) study of the type specimen described surviving material in poor condition. The “long, setaceous stipes, which arise as branches from creeping rhizomorphs" must resemble the habit of *Paramycetinis austrobrevipes*. Conversely, the following characters do not match: 1) pileus 1–2 mm broad, strongly plicate; 2) lamellae few; 3) epicutis hymeniform; 4) cheilocystidia broom cell-like. Pegler (1965) concluded: "The species clearly belongs in the genus *Marasmius*, sect. *Marasmius*."

Marasmius subsupinus Berk., in Hooker, Fl. Tasman. 2: 249, 1859 ["1860"].

From Berkeley's description the following is inferred: Basidiomata apparently conchate with a very short, curved stipe. Lamellae "so thick and rigid that this pretty species might almost be placed in *Lentinus*." "It varies in color from nearly white to rufous."

Marasmius emergens Cooke, Handb. Austral. Fungi: 88, 1892.

Protologue: "Very minute, white, suberumpent; pileus convex (1 mm broad); stem abbreviated, or sometimes elongated, curved, ascending; gills distant, few, white. On wood. Tasmania."

Marasmius subroseus Cooke & Massee, Grevillea 21: 37, 1892.

The protologue implies the following: basidiomata caespitose; no mention of rhizomorphs; "stem becoming a little reddish downwards and clad at the base with white pubescence;" gills distant. Unless proven otherwise, the organism can be accepted as a *Marasmius*.

In addition to these names, an undescribed Australian species is well-known under the informal name of *Marasmius* "angina." Online, numerous photos and one description (http://www.elfram.com/fungi/fungi_l/marspang_a.html; https://www.bushheritage.org.au/blog/fungi-and-citizen-science-in-the-liffey-valley) show an unmistakable resemblance to *Paramycetinis austrobrevipes*, except that the basidiomata are distinctly larger and no rhizomorphs appear in any photo. There is no reason (yet) to consider *Marasmius* "angina" as anything but a true *Marasmius*.

Additional specimens examined: **AUSTRALIA**, **Tasmania**, **Cradle Mountain National Park**, Waldheim Nature Track, 31.V.1991, coll. RHP & KWH, TFB 3977 (TENN-F-053232); **Geeveston**, Tahune Forest Preserve, 5.VI.1991, coll. RHP & KWH, TFB 4008 (TENN-F-050195); **Gordon-Pedder National Heritage Area**, Rainforest Nature walk vicinity, 8.VI.1991, coll. RHP & KWH, TFB 4038 (TENN-F-050212); **Hobart**, Mt. Wellington, gully at 400 m elev., 25.V.1991, coll. KWH, TFB 3591 (TENN-F-053146); coll. RHP & KWH, TFB 3585 (TENN-F-053181); **Lake Pedder National Heritage Area**, 26.V.1991, coll. RHP & KWH, TFB 3917 (TENN-F-050119); **Lake St. Clair National Park**, Mt. Rufous track, 29.V.1991, coll. RHP & KWH, TFB 3945 (TENN-F-050073); 8-10 kms north of Rosebery, slopes of Mt. Murchison, 30.V.1991, coll. RHP & KWH, TFB 3949 (TENN-F-051333); coll. RHP, TFB 3966 (TENN-F-053231).

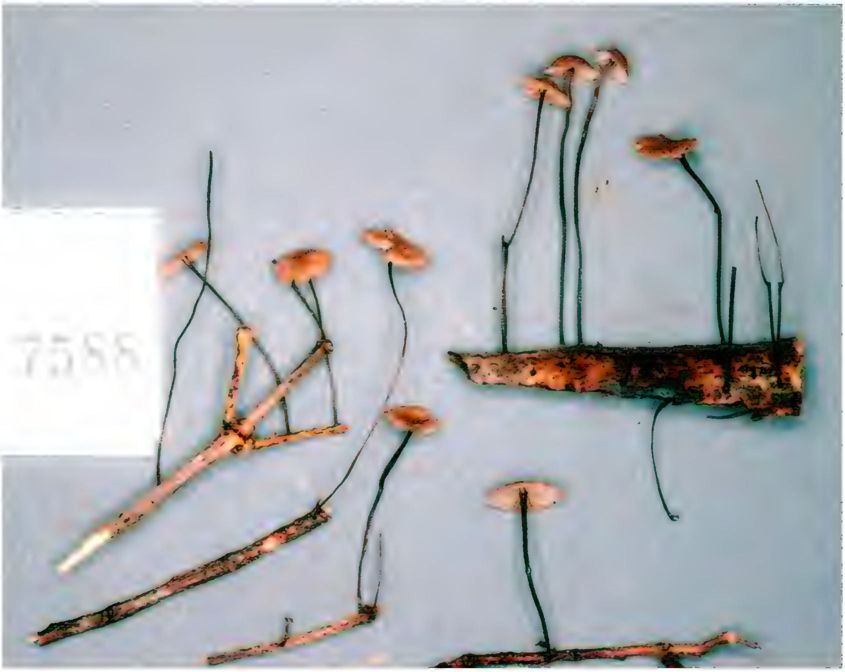

Fig. 9. *Paramycetinis caulocystidiatus* (TENN-F-053721).
Basidiomata and rhizomorphs on natural substrate.

Paramycetinis caulocystidiatus R.H. Petersen, **sp. nov.** Figs 9–14

IF 555794

Differs from *Paramycetinis austrobrevipes* by its 1) pileipellis with evidence of slime matrix; 2) high stipe length to pileus breadth ratio; 3) fruiting habit on black beech; and 4) gregarious (but separate) setoid caulocystidia.

Type: New Zealand, North Island, Urewera National Park, track to Waipai Swamp, 35°45′13″S 177°09′17″E, 27.V.1994, coll. RHP, TFB 7148 (**Holotype** TENN-F-054050).

Etymology: referring to caulocystidia of the vestured stipe.

Basidiomata (Fig. 9) slender, of medium stature, marasmioid. Pileus 2–8 (–20) mm broad, convex at first, later campanulate to applanate with depressed disc and margin remaining downturned, minutely tuberculate, translucent-striate to sulcate at margin, surface moist, hygrophanous, glabrous; central dot 8E6 ("Natal brown"), 6D6–6D5 ("snuff brown" near "olive brown"), 5D6–5D5 ("buckthorn brown"), "hazel brown," 6D8–6D4 ("buffy brown"), fading to 5C5–5C4 ("tawny olive"); limb and margin 7C4 ("wood brown") to 6C5 ("sayal brown"). LAMELLAE adnexed, suppressed and ridge-like to subventricose, subdistant, <2 mm broad, thickish, total lamellae = 35–50(–75), through lamellae = 10–17 per pileus with 1–2 ranks of lamellulae between each through-lamella, not forked or interveined, 4A2 ("pale ochraceous buff"), 5A2 ("pale cinnamon pink"), 9B2 ("vinaceous buff"), to 5B8 pastel burnt orange to near 6B3 ("tilleul buff," not white); edge entire, rounded (not sharp), not fimbriate, not marginate. STIPE 30–40(–75) × 1.3–2 mm, terete, equal (stipe base often slightly swollen), not insititious; surface moist to dry, pruinose, uniformly vestured as a turf of perpendicular setoid caulocystidia, upward 7C4 ("wood brown") to 7D5 ("Rood's brown"), downward 7E6 ("auburn"), 7E6 ("VanDyke brown"), 7F5 ("blackish brown (1)") to black; "sterile stipes" often present, 20–32 × 1–2.5 mm, straight, stiff, vestured, without pileus, occasionally decapitated (FIG. 9) and then producing rhizomorph extension (black, slender, glabrous). RHIZOMORPHS <30 × 0.2–0.7 mm (at base), glabrous, gradually narrowing to flagelliform, mostly black, only slightly paler distally, when decapitated producing a rhizomorph or stipe (glabrous versus vestured) extension, but not producing pileate basidiomata from rhizomorphs. ODOR negligible; TASTE negligible.

HABITAT AND PHENOLOGY: On dead twigs, leaves and small branches of *Nothofagus solandri*; North Island, New Zealand; May–June.

PILEIPELLIS a repent layer of generally radially oriented hyphae embedded in a thin slime matrix, tightly packed, of the following types: 1) pileal hairs (FIG. 10) <100 × 3–5 µm, perhaps erect, produced as termini of repent hyphae (FIG. 11) finely encrusted, usually subtly capitulate; 2) repent hyphae 2–8(–13) µm diam, at surface usually of the wider type, firm-walled, coarsely encrusted in thick scabs; profile calluses ≤2 µm thick, sub-refringent (PhC); crust material often distributed with suggestion of striped or annular thickenings; 3) repent hyphae 5–10 µm diam with gelatinizing walls (wall ≤2.5 µm thick), variously encrusted; 4) subpellis hyphae usually thicker (6–14 µm diam), smooth or with very fine encrustation appearing gritty on the hyphal surface; clamp connections ubiquitous. PLEUROCYSTIDIA (FIG. 12) 24–32 × 6–9 µm, common, broadly fusiform, conspicuously clamped; contents homogeneous to distinctly partitioned. BASIDIA 25–30 × 7–11 µm, clavate, often sub-urniform, 4-sterigmate, clamped; effete basidia (and pleurocystidia) do not disappear but leave residual lateral walls and shriveled sterigmata ("husking"). BASIDIOSPORES (5–)6.5–8(–9) × 3.5–4(–4.5) µm ($Q = 1.43–2.43$; $Q^m = 1.92$; $L^m = 7.41$ µm), ellipsoid, somewhat flattened adaxially, smooth, thin-walled, inamyloid. CHEILOCYSTIDIA (FIG. 13) hardly distinguishable from basidia,

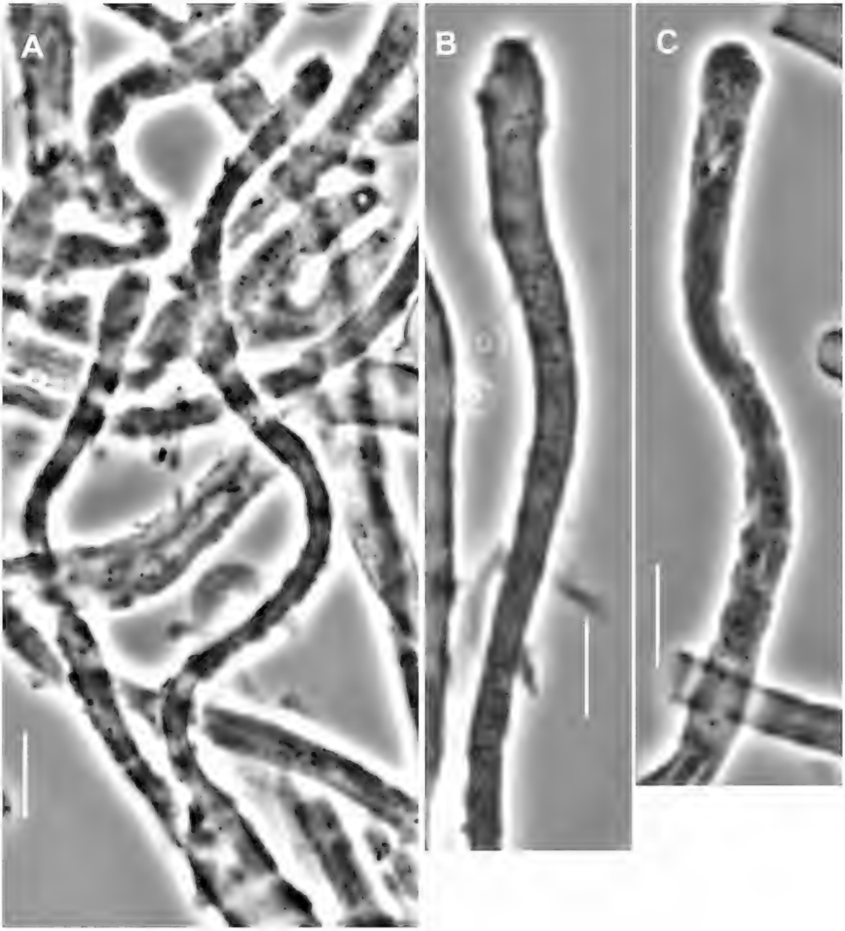

Fig. 10. *Paramycetinis caulocystidiatus* (TENN-F-054050).
Pileal hairs. A. Origin of two pileal hairs. B,C. Individual pileal hairs. Scale bars: 10 µm.

29–35(–42) × 6–13 µm, broadly truncate-clavate, hardly lobed apically, obscurely clamped. Stipe medullary hyphae 3–9 µm diam, strictly parallel, adherent with minimal slime matrix, thin-walled inward, with gelatinizing walls (<2.5 µm thick) near cortex, obscurely clamped, hyaline, inamyloid inward, increasingly dextrinoid toward stipe surface (to moderately so in Melzer's reagent + BF). Stipe cortical hyphae strictly parallel, probably coherent and perhaps with thin slime layer, coarsely encrusted, thick-walled, yellow-brown

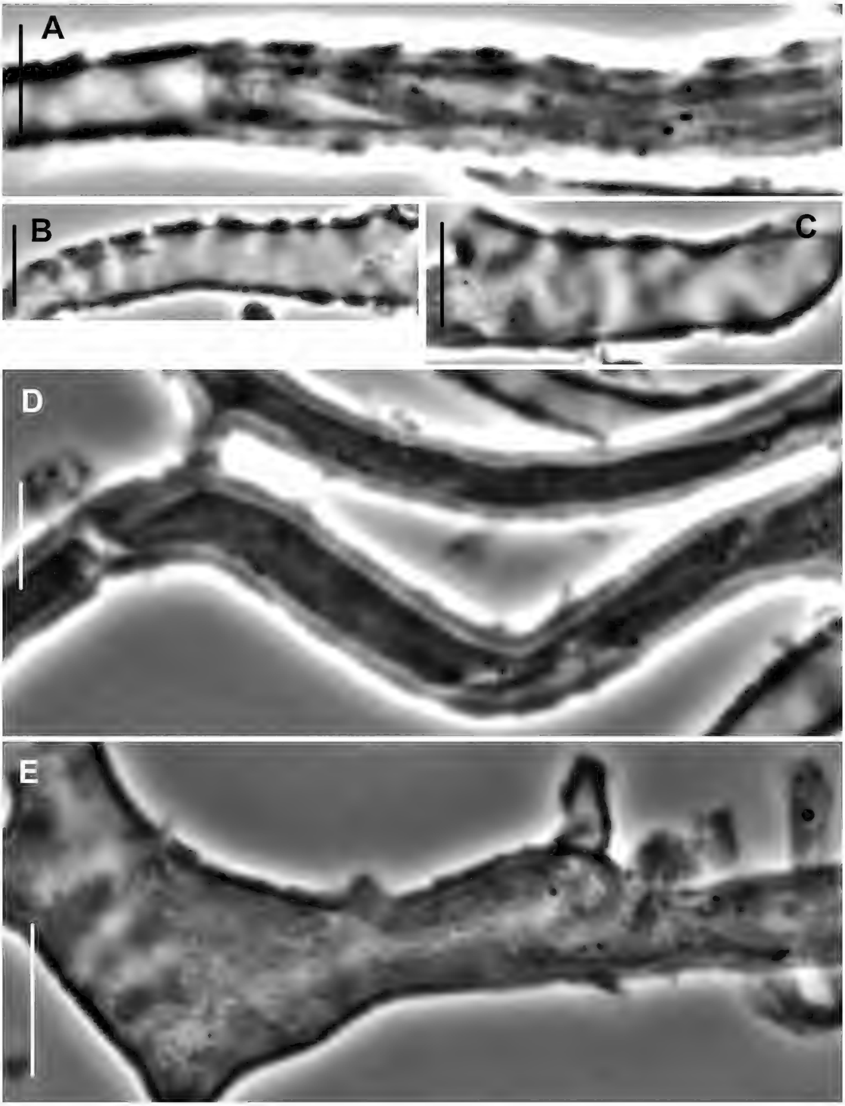

Fig. 11. *Paramycetinis caulocystidiatus* (TENN-F-054050). Pileipellis elements. A. Heavily encrusted hypha with gelatinized wall. B,C. Encrusted hyphae with suggestion of striped or annular ornamentation. D. Hyphae with gelatinized walls. Note anastomosis in "H"-connection. E. Swollen subpellis hypha. Scale bars: 10 µm.

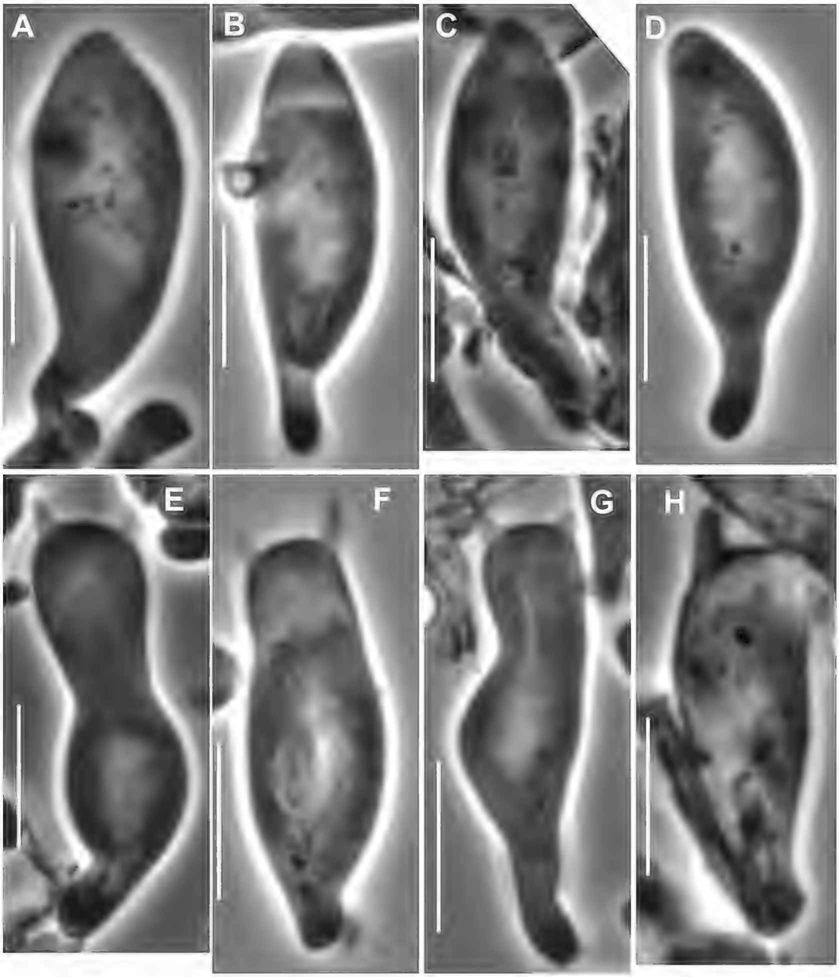

Fig. 12. *Paramycetinis caulocystidiatus* (TENN-F-054050). Hymenial elements. A-D. Pleurocystidia. B. Note partitioned contents. E–H. Basidia. Scale bars: 10 µm.

(PhC), dark red-brown in Melzer's reagent + BF. Caulocystidia (Fig. 14) arising as side branches from thick-walled, smooth, superficial cortical hyphae, stiff, setoid, arising as short lobes (and then hyaline), elongating >70 × 6–9 µm at base, 3–4.5 µm diam at apex, narrowly rounded, thick-walled (wall ≤3 µm thick when visible), sub-refringent and hyaline distally (150× + PhC), strongly dextrinoid (red-brown in Melzer's reagent + BF; dark red-brown in Melzer's reagent + PhC).

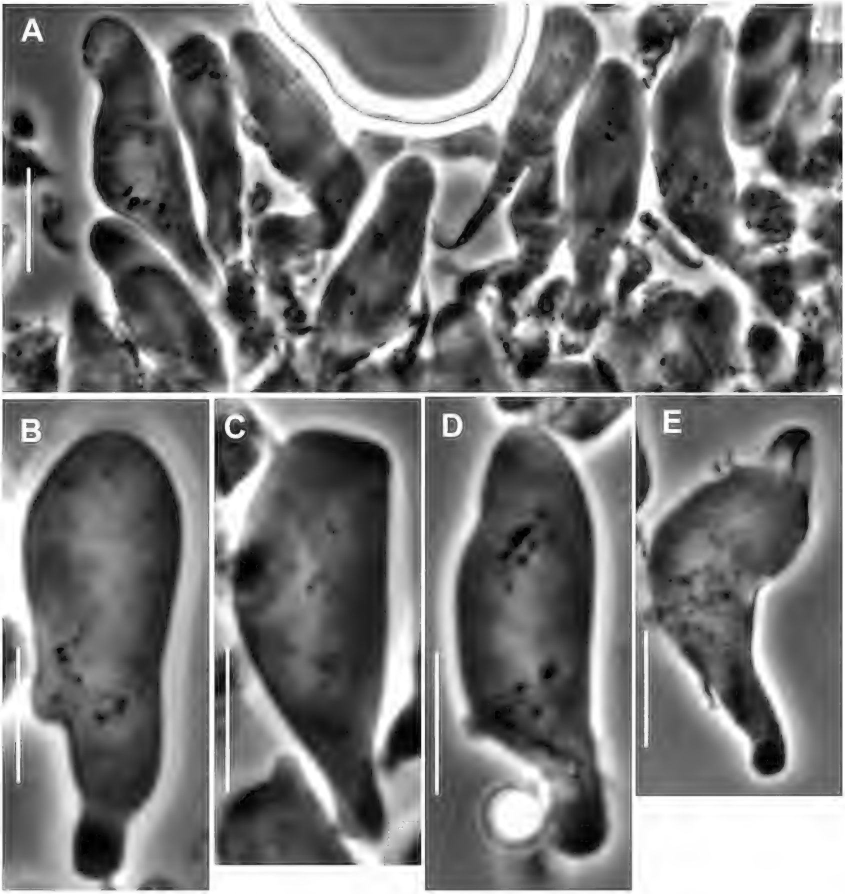

Fig. 13. *Paramycetinis caulocystidiatus* (TENN-F-054050). Cheilocystidia.
A. Grouped at lamellar edge. B–E. Individual cheilocystidia. Scale bars: 10 µm.

Commentary: Pileipellis structure is typical of *Gymnopus* sect. *Perforantia.* Hyphal types match quite well, especially gelatinizing hyphal walls and presence of pileal hairs, and there is evidence of a thin slime matrix. Stipe to pileus ratio is high, with the stipe universally vestured and minutely barbed. Dried pileus now somewhat campanulate, with umbo slightly darker than limb or margin; pileus now appearing somewhat moist-laccate. Basidiomata are accompanied by thin, ascendant rhizomorphs. The "omnipotent" stipes and rhizomorphs are somewhat unique, and are quite obvious as abrupt, odd, asymmetrical joints of such structures (see Fig. 9).

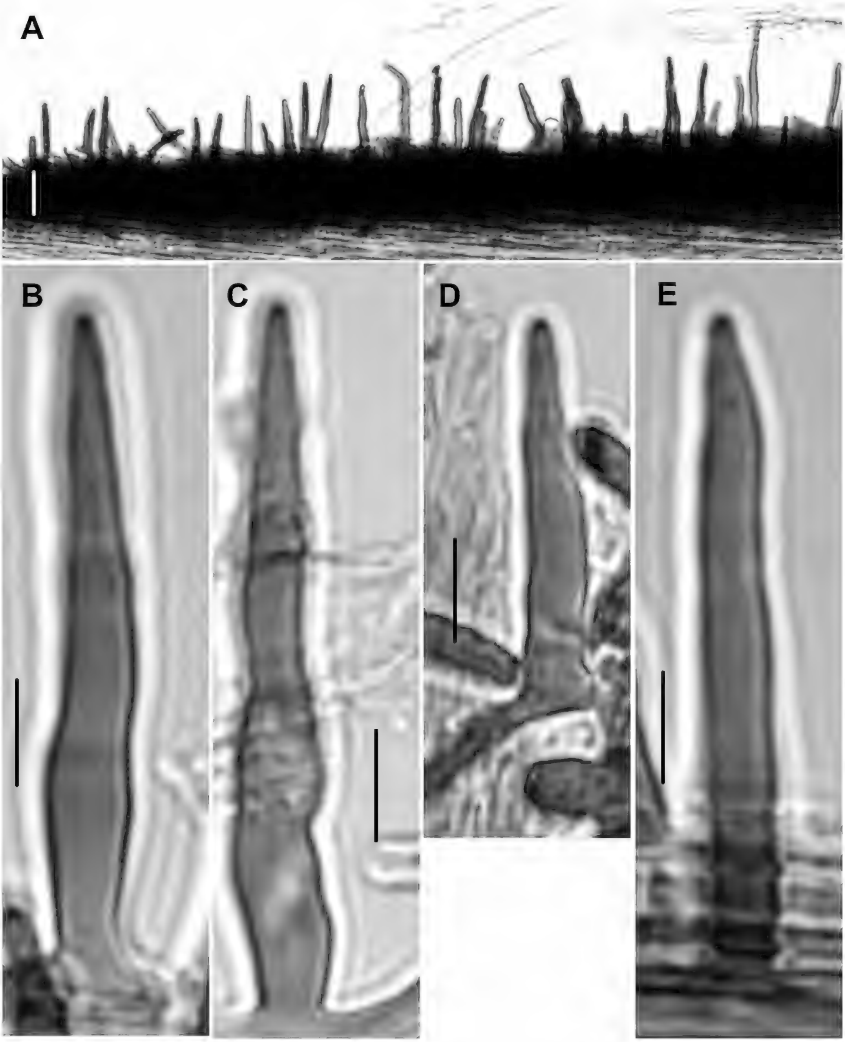

Fig. 14. *Paramycetinis caulocystidiatus* (TENN-F-054050). Caulocystidia.
A. Overview of stipe surface; note gregarious but separate individual caulocystidia.
B–E. Individual caulocystidia. Scale bars: A = 20 µm; B–E = 10 µm.

Paramycetinis caulocystidiatus joins *Pa. austrobrevipes* in a small clade sister to that of *Mycetinis* (Fig. 1). The latter is characterized by a roughly hymeniform pileipellis of inflated, naked, thin-walled cells and usually a basidiomatal alliaceous odor and taste. Wilson & Desjardin (2005) showed that

Mycetinis taxa were found embedded among taxa of *Gymnopus* s.l. and assorted other genera. Petersen & Hughes (2017b) surveyed *Mycetinis*, with a detailed ITS-based phylogeny of the genus.

On whole wheat flour agar (Farnet & al. 1999), cultures of *Pa. caulocystidiatus* produced no textura intricata, white to off-white felty mycelium, and no rhizomorphs.

ADDITIONAL SPECIMENS EXAMINED: **NEW ZEALAND, NORTH ISLAND, Urewera National Park**, Lake Waikaremoana, Black Beech Track, 28.V.1994, coll. A.S. Methven, TFB 7588 (TENN-F-053721); Lake Waikareiti Track, 27.V.1994, coll. A.S. Methven, TFB 7572 (TENN-F-053683).

Pseudomarasmius

Oliveira & al. (2019) resolved a clade they named /pallidocephalus (not a genus name). It is this clade that we propose as *Pseudomarasmius*. They encouraged generic status for the clade which, they admitted, needed more research.

Oliveira & al. (2019) proposed *Pusillomyces*, closely related to *Gymnopus asetosus* and *G. funalis* (their clade B). *Pusillomyces manuripioides* (typus generis) was described as lacking clamp connections, a trait virtually diagnostic for *Pseudomarasmius*, proposed here, but relatively unrelated to their clade B.

A PhyML analysis of nrITS sequences for species within *Pseudomarasmius* is given in FIG. 15 and broader placement based on the nrLSU region is given in FIG. 1. *Pseudomarasmius* comprises several species and an unidentified clade of fungal soil isolates from Guyana.

Pseudomarasmius R.H. Petersen & K.W. Hughes, **gen. nov.**

IF 317324

Differs from *Marasmius* by 1) diverticulate hyphae present in the pileipellis and 2) clamp connections absent.

TYPE SPECIES: *Pseudomarasmius pallidocephalus* (Gilliam) R.H. Petersen

ETYMOLOGY: Referring to its similarity to *Marasmius.*

Basidiomata of three types: 1) similar in size and stature to those of *Gymnopus* sect. *Androsacei*, with discrete, bristle-like stipe and convex to applanate cap; rhizomorphs slender and inconspicuous limited to rotting leaf or needle litter; 2) similar in size and shape to those of *Marasmiellus*, with small, curved stipe and shell-like pileus and usually dominant rhizomorphs which occasionally produce basidiomata as side branches, similar to this phenomenon in *Marasmius crinis-equi*; and 3) small, slender, pallid yellowish mycenoid basidiomata lacking rhizomorphs, on rotting needles of *Abies* or *Picea*. Microstructures resembling those of *Gymnopus* sect. *Androsacei* and *Marasmius* sect. *Sicci*, including: 1) diverticulate hyphae in pileipellis (arranged in a "rameales-structure"); 2) thick-walled, gelatinizing hyphae and/or gelatinizing diverticulate hyphae in pileipellis and subpellis; 3) without clamp connections or clamps rare and restricted to pileus trama; 4) basidia (2–)-4-spored; 5) spores similar to those of other gymnopoid genera, ellipsoid, thin-walled, inamyloid; 6) molecular (LSU, ITS) profiles unique, grouping into a monophyletic clade related to *Rhodocollybia* but more distant from groups exhibiting similar basidiomatal types (Fig. 15).

Key to species of *Pseudomarasmius*

1. Ratio of pileus breadth to stipe length <2 ("thumb-tack shaped"); basidiomata small, often arising as side branches of rhizomorphs 2
1. Ratio of pileus breadth to stipe length >4; basidiomata marasmioid or mycenoid, arising as rhizomorph branch or independently on leaf litter or woody substrate 3

2. Southern South America (Isla Chiloé, Chile); rhizomorphs inconspicuous, not producing basidiomata; fruiting on hardwood substrates; clamp connections absent; superficially inseparable from *Ps. nidus-avis* . . . . ***Ps. patagonianus***
2. North American Gulf Coastal Plain and subtropical eastern Mexico; rhizomorphs dominant, long, occasionally branched, occasionally producing basidiomata as side branches; fruiting on small dead branches and twigs of deciduous trees usually at some distance from the ground; clamp connections occasional in rhizomorphs and tramae but otherwise absent . . . . ***Ps. nidus-avis***

3. Antipodal (New Zealand); basidiomata minute (pileus 1–3.5 mm broad; stipe capillary, 6–8 mm long); fruiting on hanging dead terminal branches of *Dacrydium;* . . . . ***Ps. efibulatus***
3. Not Antipodal; fruiting substrate leaf or needle litter 4

4. Fruiting on conifer needle litter; rhizomorphs usually inconspicuous 5
4. Fruiting on hardwood leaf litter (including *Castanopsis*); rhizomorphs conspicuous, resupinate on leaf surface 7

5. Temperate to northern North America; stipe black; basidiomata like those of *Gymnopus* sect. *Androsacei* (pileus <35 mm broad; stipe 12–43 × 0.2–0.8 mm); pileus white to off-white; rhizomorphs inconspicuous, usually found deep in humus . . . . ***Ps. pallidocephalus***
5. South Korea/eastern North America; basidiomata slender, mycenoid; stipe ochraceous to straw-colored; 6

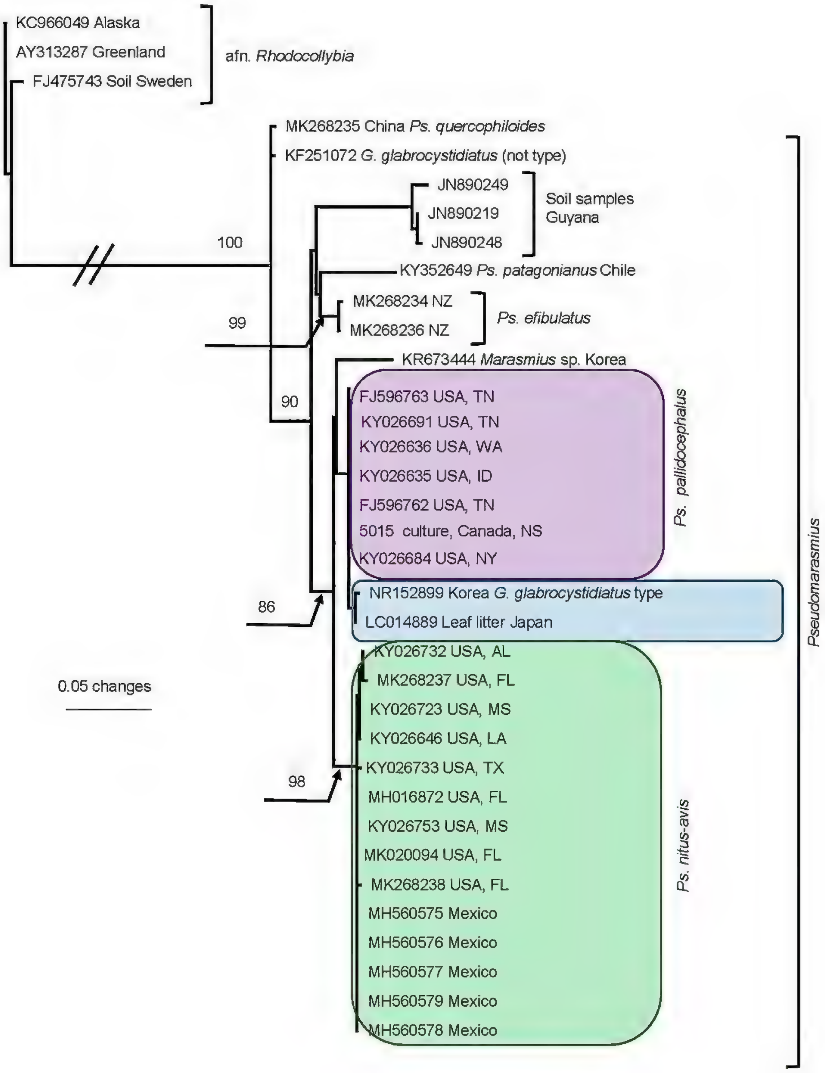

FIG. 15. Maximum likelihood analysis of ribosomal RNA ITS sequences. Bootstrap values are given to the left of the supported node. Numbers are GenBank accession numbers (See TABLE 1). For collections from the United States and Canada, the state or province postal code is given. NZ = New Zealand.

6. South Korea (and probably Japan); basidiomata minute, fragile
 (pileus 48 mm broad; stipe 15–40 × 0.5 mm); pileus dark grey-green;
 stipe dark brown to black-brown; rhizomorphs inconspicuous;
 fruiting on dead needles of *Abies*. . . . . **Ps. glabrocystidiatus**

6. Eastern North America; basidiomata similar to those of *Ps. glabrocystidiatus*;
 pileus light brown or pale greyish brown; stipe brownish orange to yellow
 or straw-colored; on rotting needles of *Picea* and *Abies* . . . . **Ps. straminipes**

7. Costa Rica; high-altitude *Quercus* forests . . . . **Ps. obscurus**

7. South Korea, China (Yunnan); on dead leaves of *Castanopsis* . . . **Ps. quercophiloides**

Pseudomarasmius efibulatus R.H. Petersen, **sp. nov.** Figs 16–20

IF 555730

Differs from *Pseudomarasmius* taxa by its: 1) minute basidiomata; 2) fruiting habit on dead *Dacrydium* branchlets; 3) scattered pyramidal to digitate diverticula on pileipellis elements; 4) known distribution limited to the New Zealand type location.

Type: New Zealand, South Island, Westland, Fox Glacier, Lake Matheson loop trail, 43°26′22″S 169°57′54″E 13.V.1994, coll. RHP, TFB 7070 (TENN-F-056187).

Etymology: from *fibula* (Latin) for clamp, buckle + *e-* (Latin), without. Referring to the clampless condition.

Basidiomata (Fig. 16a) diminutive. Pileus 1–3.5 mm broad, convex when young, becoming everted by maturity, matte, pebbled; disc 7C5 (“fawn color”), outward 9B2 (“vinaceous buff”) to 6A3 (“pinkish buff”). Lamellae adnate, arcuate, not collariate, thickish, c. 1 mm broad, not marginate, off-white when fresh, becoming 5A4 (“light ochraceous buff”) over time; lamellulae occasional, short; total lamellae (10)1218; through lamellae 7–8. Stipe 6–8 × 0.2–0.4 mm, apically 8E6 (“Natal brown”) (and this color extending through lamellar attachment to pileus flesh), lower 7/8 black, glabrous-shining, insititious. Rhizomorphs (Fig. 16a,17) common, <40 × 0.1–0.3 mm, more or less straight (not curly), rarely branched, arising separately from basidiomata.

Habitat and phenology: On dead, pendant *Dacrydium* foliage; Autumn.

Pileipellis with minimal slime matrix and composed of the following: 1) diverticulate hyphae (Fig. 18a–d) 4.5–10 µm diam, thin-walled, with scattered diverticula ≤10 × 1.52 µm (often c. 4 µm diam at base and therefore more or less pyramidal), often dichotomous or saddle-shaped, not refringent [in fact appearing darker than the parent hyphae in PhC]; 2) broom cell-like termini (Fig. 18e–h) 15–25 × 9–16 µm, stalked, usually dichotomously branched, surmounted with rows of diverticula; diverticula 3–8 × 1–1.5 µm, hardly refringent (PhC). Pileus tramal hyphae 3–6 µm diam, firm-walled, long-celled, apparently without clamp connections; wall somewhat obscure,

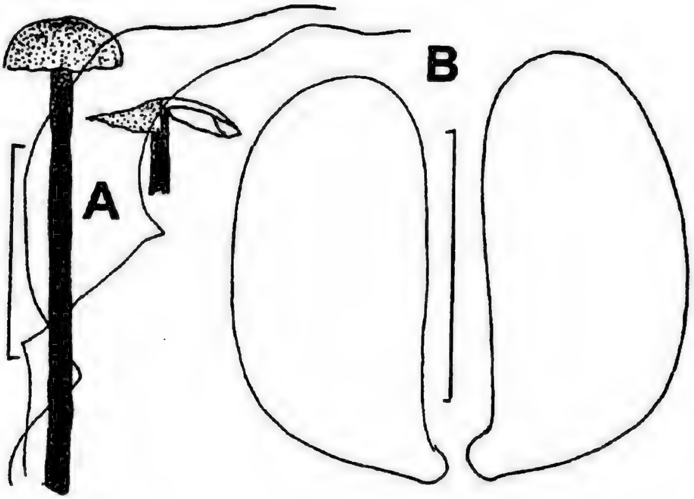

Fig. 16. *Pseudomarasmius efibulatus* (TENN-F-056187, holotype).
A. Basidiomata and rhizomorphs. B. Basidiospores. Scale bars: A = 5 mm; B = 5 µm.

as though semi-gelatinized. Lamellar tramal hyphae similar. Hymenium apparently involved in minimal gelatinized matrix (excessive hymenial remnants and other debris). Pleurocystidia (Fig. 19a–d) 24–30 × 6–7 µm, fusiform, often irregularly so, without content partitioning or clamp connection. Basidioles clavate, usually subcapitulate; Basidia (Fig. 19e–h) 22–30 × 6–9 µm, clavate, 4-sterigmate, without clamp connections. Basidiospores (Fig. 16b) (7–)7.5–11 × 3.5–4.5 µm (Q = 2.053.14; Q^m = 2.26; L^m = 8.67 µm), elongate-ellipsoid to subcylindrical, more or less marasmioid (somewhat tapered proximally), flattened somewhat adaxially, thin-walled, smooth, inamyloid. Lamellar edge apparently fertile. Cheilocystidia (Fig. 20) widely scattered, 22–35 × 10–12 µm, stalked-clavate to saccate, entire or with a few slender, digitate apical processes, without clamp connections. Stipe medullary hyphae 1.5–12 µm diam, strictly parallel, involved in a slime matrix, thin- to thick-walled (wall c. 0.7 µm thick, hyaline), distinctly without clamp connections, relatively short-celled; subcortical hyphae 4–8 µm diam, thick-walled (wall c. 1.5 µm thick), strongly refringent, yellow (PhC). Stipe cortical hyphae 4–7 µm diam, firm-walled, short-celled, without clamp connections, pigmented yellow-olive (PhC); surface minutely roughened with dried thin slime. Caulocystidia absent.

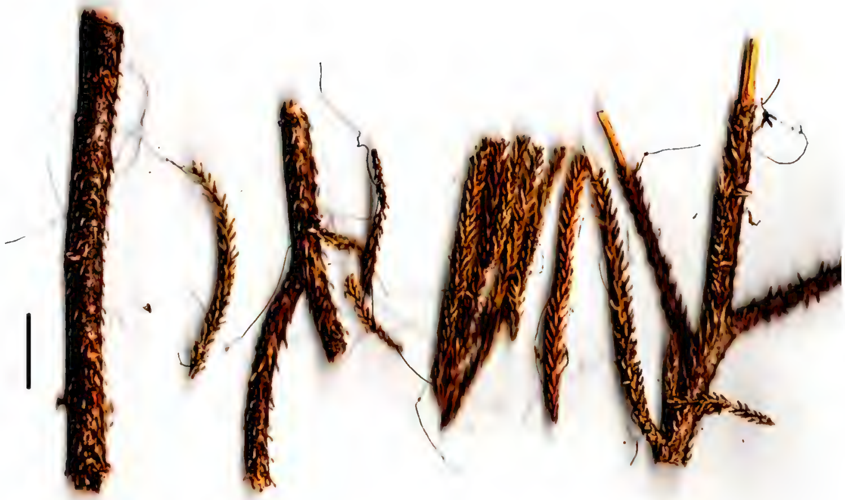

Fig. 17. *Pseudomarasmius efibulatus* (TENN-F-056187, holotype). *Dacrydium* branchlets with rhizomorphs. Scale bar = 10 mm.

Commentary: Based on ribosomal nrRNA ITS sequences, *Ps. efibulatus* is related to but distinct from *Ps. pallidocephalus*, *Ps. glabrocystidiatus*, and *Ps. nidus-avis*. It is closely related to sequence JAC10695 received from J. Cooper, Landcare Research, New Zealand (Fig. 15)

A blast of ITS sequence from *Ps. efibulatus* (TFB 7070, TENN-F-056187) showed an affinity with ITS sequences of *Ps. glabrocystidiatus*, a clampless taxon from South Korea, placed by its authors in *Gymnopus* sect. *Androsacei.* Sequences of *Ps. glabrocystidiatus* are virtually congruent to those of *Ps. pallidocephalus* (see above) found frequently across northern North America fruiting on dead conifer needles, also the habit of the Asian *G. glabrocystidiatus*. The nrITS-based phylogeny produced by Antonín & al. (2014) placed *G. glabrocystidiatus* within *Gymnopus* but on a long, independent branch described as part of *G.* sect. *Androsacei.* The nrLSU-based phylogeny in Fig. 1 (above) indicates even more significant isolation of *Pseudomarasmius*.

Pseudomarasmius efibulatus belongs to a small complex of similar, slender, gracile basidiomata along with *Ps. straminipes* and *Ps. glabrocystidiatus*, but the basidiomata of all three species are so small and inconspicuous as to be

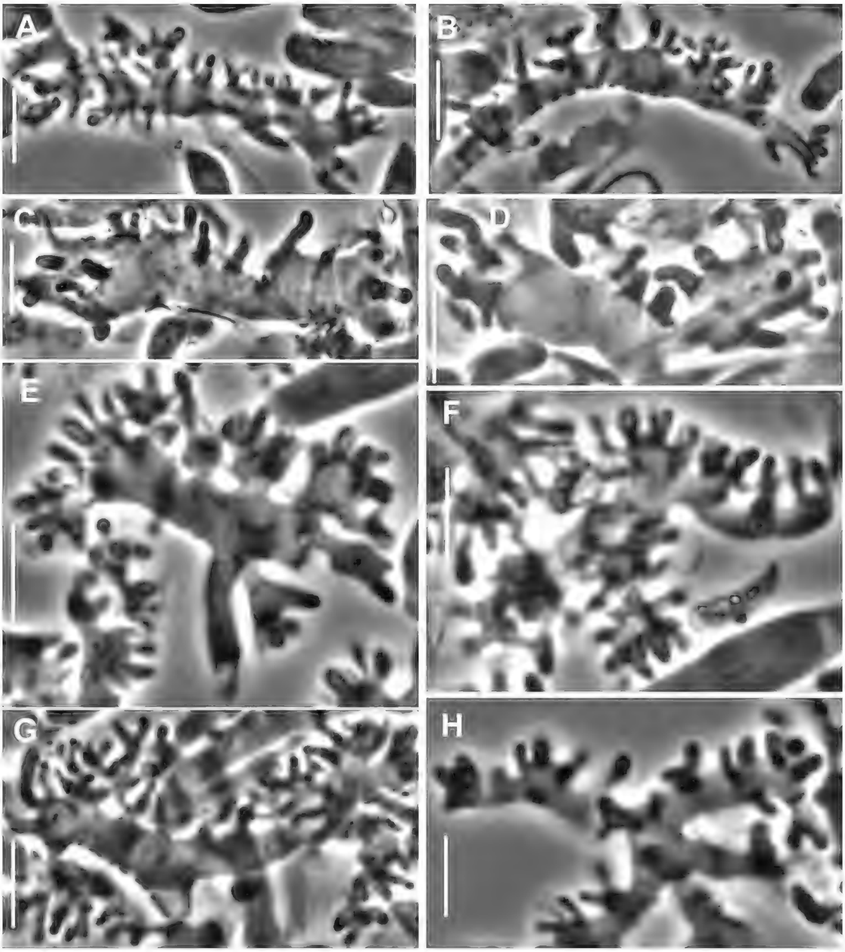

Fig. 18. *Pseudomarasmius efibulatus* (TENN-F-056187, holotype). Pileipellis elements. A–D. Diverticulate hyphae. E–H. Broom cell-like hyphal termini. Scale bars: 10 µm.

easily overlooked. *Pseudomarasmius efibulatus,* however, is quite isolated in substrate and distribution.

The few similarities between *Ps. pallidocephalus* and *Ps. efibulatus* include: 1) clampless condition; 2) temperate distribution (North- and South-Temperate climates); 3) stipe without caulocystidial ornamentation; 4) a complex "*ramealis*-structure" of pileipellis; 5) cheilocystidia that are usually smooth, broadly clavate or ampulliform; and 6) well-developed rhizomorphs.

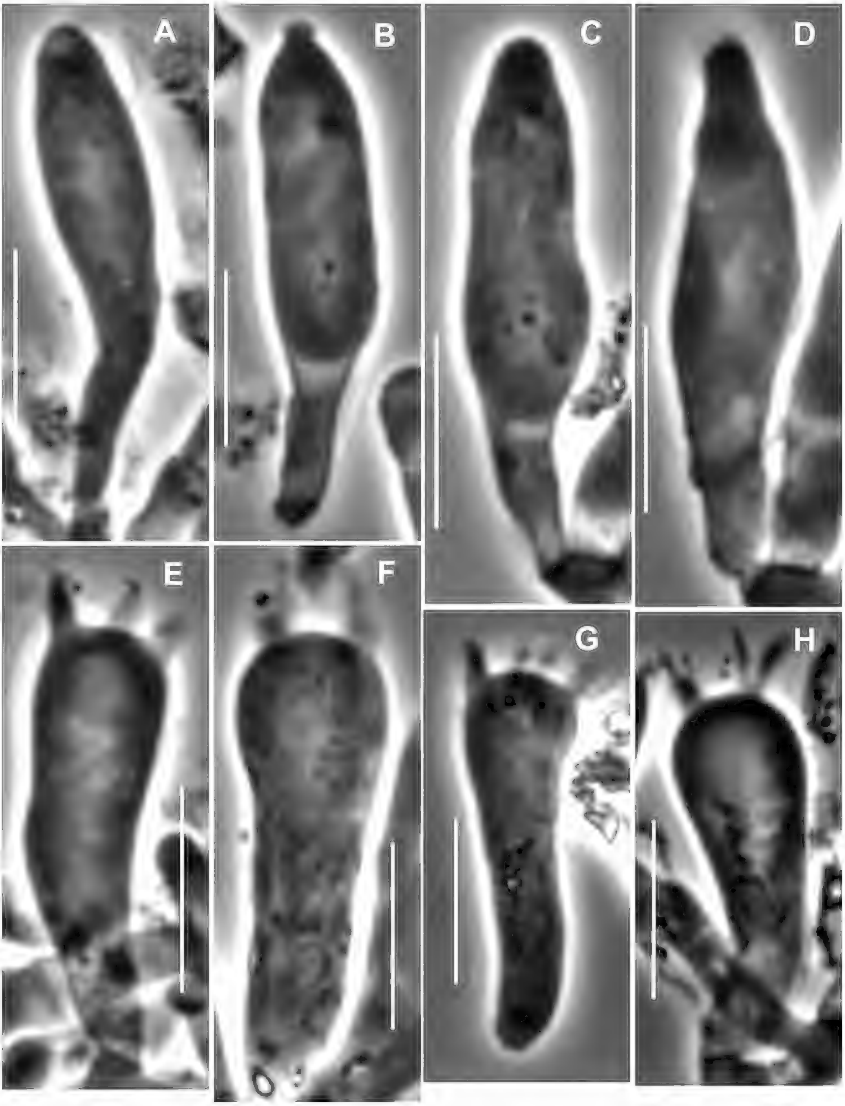

FIG. 19. *Pseudomarasmius efibulatus* (TENN-F-056187, holotype). Hymenial elements. A–D. Pleurocystidia. E–H. Basidia. Scale bars: 10 µm.

Basidiospores are smooth, ellipsoid to elongate pip-shaped, and white in spore deposits throughout the /gymnopus/marasmiellus clade, with spore measurements distinguishing the taxa reported as follows: *Ps. efibulatus* = (7–)7.5–11 × 3.5–4.5 µm (Q = 2.26); *G. glabrocystidiatus* = (7.7–)8.5–9.5

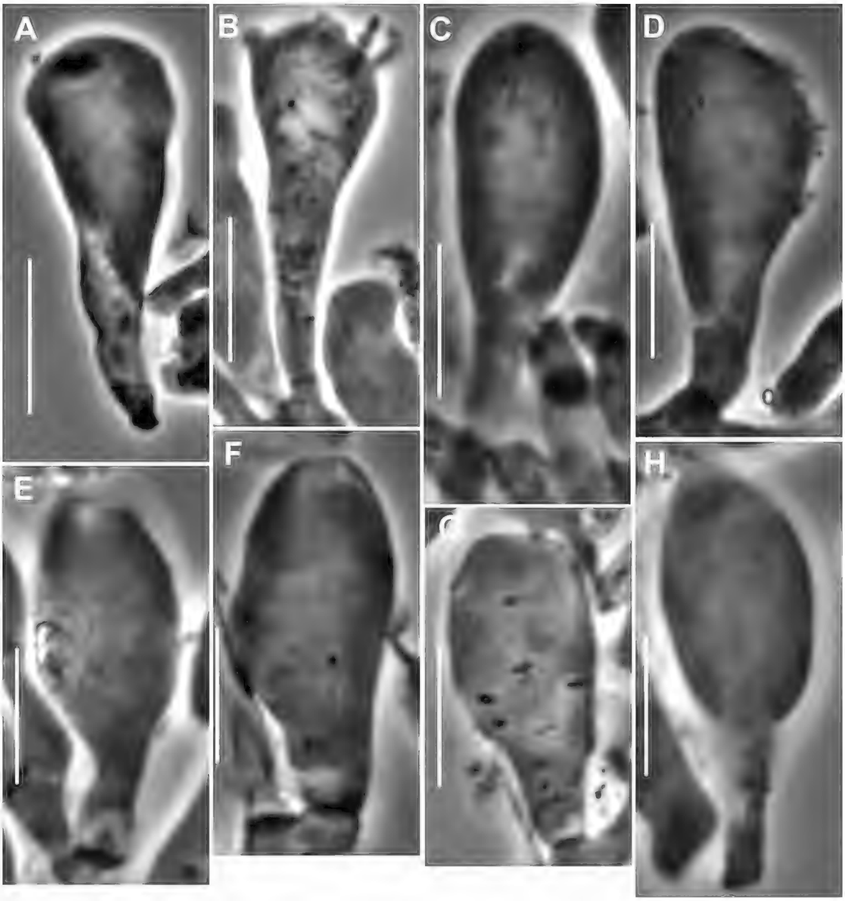

Fig. 20. *Pseudomarasmius efibulatus* (TENN-F-056187, holotype). Cheilocystidia. Scale bars: 10 µm.

(–10) × 4–5 µm (Q = 2); *Ps. pallidocephalus* = (5–)5.5–7(–9.5) × 3–3.5 µm (Q = 1.87).

Macroscopically, basidiomata of *Ps. nidus-avis* and *Ps. patagonianus*, superficially resemble numerous *Marasmiellus* taxa fruiting on dead twigs and small branches of deciduous trees and exhibiting extensive, robust rhizomorphs. Although morphologically counterintuitive for inclusion in *Pseudomarasmius*, ITS- and LSU-based phylogenies place *Ps. nidus-avis* and *Ps. patagonianus* with the other taxa in the genus.

Perhaps most surprising about the sole collection of *Ps. efibulatus* was the absence of clamp connections. Collections of similar basidiomata found fruiting on the same somewhat unique substrate demonstrated ubiquitous clamp connections. Moreover, pileipellis elements of clamped and clampless organisms compare well: a complex pileipellis composed of both repent diverticulate hyphae (with diverticula often bifurcate) and broom cell-like hyphal termini beset with diverticula also often dichotomous. This may be analogous to the situation in *Ps. straminipes* (clampless) and its form *fibulatus* (clamp connections ubiquitous). DNA sequences not currently extant may help to clarify this situation.

Pseudomarasmius glabrocystidiatus (Antonín, Ryoo & Ka) R.H. Petersen, **comb. nov.** FIGS 16–20

IF 555747

≡ *Gymnopus glabrocystidiatus* Antonín, Ryoo & Ka, Mycol. Prog. 13(3): 710. 2014. Republic of Korea, Inje, Baekdam-sa, 27. VI. 2008 leg. V. Antonín (08.36), R. Ryoo & J.G. Han (**Holotype**, BRNM 718676).

ADDITIONAL PUTATIVE CONTAXIC COLLECTION (but see below): Culture. Korea, Jeju, Seonheul-gotjawal, 06.IX.2012, R. Ryoo, K.-H. Ka & H.D. Sou (KFRI 1935).

For detailed description and illustrations see Antonín & al. (2014)

Major distinguishing characters include: 1) basidiomata similar to those of *Ps. straminipes*; 2) clamp connections absent; 3) pileus dark (grey-)brown with paler margin when young, then brownish at center and paler, beige to pale brown at margin; 4) basidia 2- spored; 5) stipe smooth and glabrous, dark brown to black-brown; 6) cheilocystidia smooth, clavate or pyriform; 7) pileipellis composed of more or less smooth or diverticulate hyphae and single broom cells; 8) habitat on dead conifer (*Abies*) needles; 9) geographic distribution, South Korea (probably Japan).

HABITAT: needles of *Abies holophylla*.

COMMENTARY: In the phylogeny presented by Antonín & al. (2014), two ITS sequences of putative *Gymnopus glabrocystidiatus* (GB NR152899, holotype; KF251072, ancillary sequence from culture) appeared in a single small clade but on individual short branches. This clade appears sister to *Rhodocollybia*, a position similar to that shown on our LSU-based phylogeny (FIG. 1) for *Pseudomarasmius*. An ITS sequence from holotype material of *G. glabrocystidiatus* differs from those of *P. pallidocephalus* by 31/694bp (4.46%) and while apparently in the same clade based on nrITS sequences alone (FIG. 15), nrITS sequence divergences warrant separate species designations. Further, *G. glabrocystidiatus* is an Asia taxon while

Ps. pallidocephalus is North American in distribution. The description and illustrations of *Ps. glabrocystidiatus* furnished by Antonín & al. (2014) are adequate and require no enhancement here.

Although two GenBank designations for ITS sequences of *G. glabrocystidiatus* were reported in the phylogeny by Antonín & al. (2014), KP251073 ("NR152898" from holotype material) and KP251072, the latter can be traced to a culture from an ancillary specimen apparently misidentified. The two sequences appear only distantly related in our ITS-based phylogeny (Fig. 15).

The non-type GenBank sequence (KF251072) virtually matches that of TFB 3162, here proposed as *Ps. quercophiloides* (q.v.). The latter was collected in China.

GenBank sequence LC014889, including the ITS region, was derived from an environmental sample from leaf litter of *Picea jezoensis* subsp. *hondoensis* (spruce) in Funabashi, Japan (Hagiwara & al. 2015). The sampling site was in central Honshu Island (35 36'N, 13728'E) and dealt with bleaching of substrate leaf debris, including conifer (Hintikka 1970; Miyamoto & al. 2000; Osono 2015). The spruce substrate generally agrees with that of *Ps. glabrocystidiatus* and, with the latter distribution in South Korea (Antonín & al. 2014), the Japanese report seems within the ecological pattern for the complex.

Pseudomarasmius nidus-avis (César, Bandala & Montoya) R.H. Petersen, **comb. nov.** Figs 21–31

IF 555746

≡ *Gymnopus nidus-avis* César, Bandala & Montoya, Mycokeys 43: 25. 2018

Type: Mexico. Veracruz: Municipality of Xalapa, Santuario del Bosque de Niebla, Instituto de Ecología A.C., 1343 m a.s.l., gregarious, on fallen twigs of *Quercus*, 20 April 2016, Cesar 36 (Holotype, XAL).

Diagnostic characters include 1) basidiomata that are small and thumb tack-shaped, often arising as side branches from rhizomorphs; 2) a short, curved stipe; 3) distribution in North American Gulf Coast and subtropical Mexico; 4) clamp connections lacking except rare in stipe medulla.

Basidiomata (Figs 21, 22) arising from woody substrate or (more often) as side branches of rhizomorphs. Pileus 2–6(2–10) mm broad, convex to plano-convex, usually somewhat depressed over the disc, occasionally shallowly umbonate, pulvinate, variously sulcate-striate, matt, uniformly more or less "wood brown" (7C4), pale brown (7.5 YR 7/4–6; 10YR 7/4; Munsell) to brown (7.5 YR 5/6; 10 YR 4/4; Munsell); context thin (<1 mm

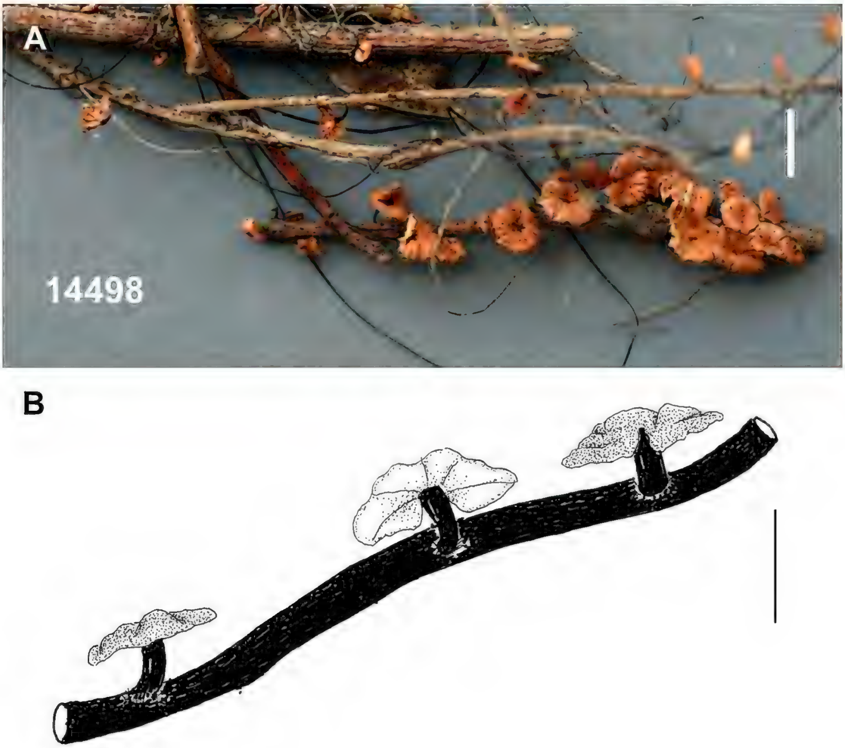

Fig. 21. *Pseudomarasmius nidus-avis* (TENN-F-054912). Basidiomata. A. Habit photo. B. Basidiomata, macromorphological aspect. Scale bars: 10 mm.

thick), soft, whitish. Lamellae (<1 mm broad; 13–26 total lamellae, 4–9 through lamellae, anastomoses lacking), adnate, adnexed to shallowly subdecurrent, thick with rounded edge, paler than pileus surface, ivory to off-white when fresh, very pale brown (2.5 Y 8/2; Munsell)], after drying suffused ruddy brownish outward from stipe (now "wood brown" 7C4, or "avellaneous" 7B3); lamellar edge entire. Stipe arising either from woody substratum or as side branches of rhizomorphs; 2–6(–12) × (0.2–)0.7(–1.6) mm, central to slightly eccentric, terete, equal or tapered downward, black, glabrous-shining, straight to strongly curved, insititious, reddish-brown at the apex (2.5 YR 4/6; Munsell), dark brown to black below (10YR 2/1, 7.5YR 2.5/2; Munsell), brown; medulla light brown (2.5Y 6/4; Munsell;

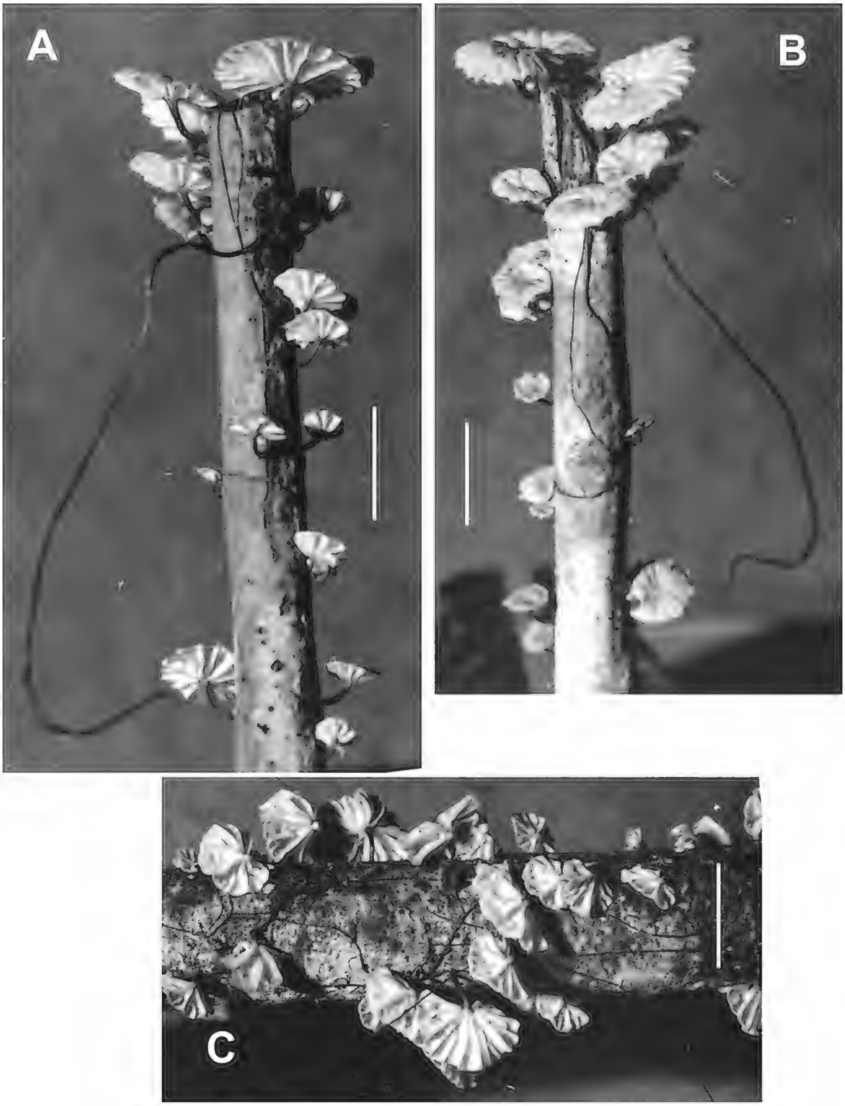

Fig. 22. *Pseudomarasmius nidus-avis* (TENN-F-047666). Basidiomata. Scale bars: 10 mm. Photos courtesy David P. Lewis.

basal tuft very sparse). Rhizomorphs (Fig. 21, 22a,b) ≤500 × 0.1–0.3 mm, simple, black, wiry, abundant, black, glabrous-shining. Taste and odor not distinctive.

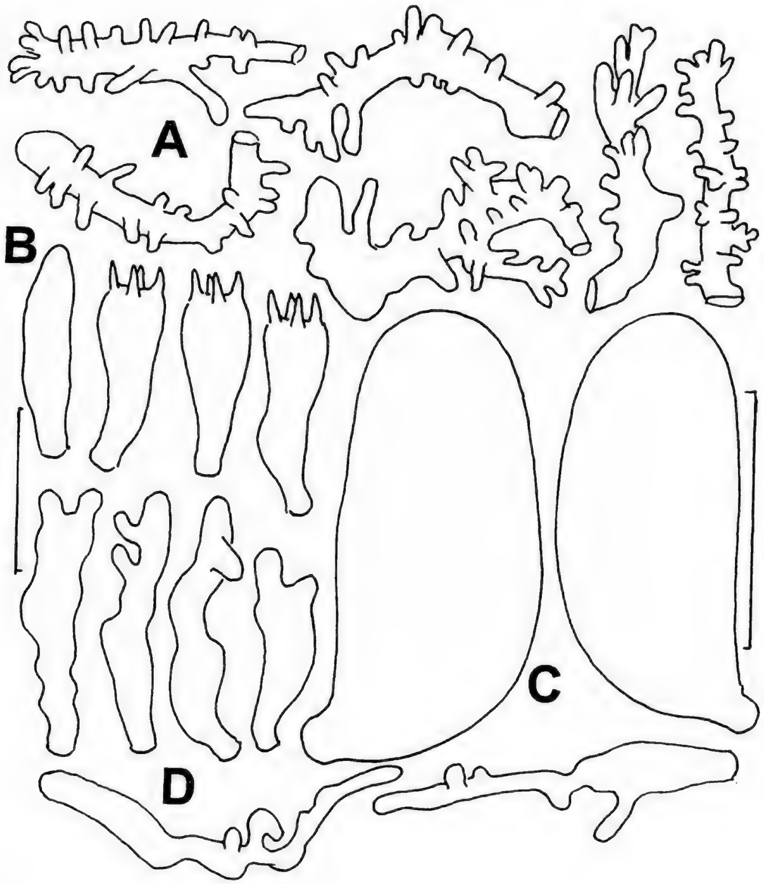

Fig. 23. *Pseudomarasmius nidus-avis* (TENN-F-054912). Micromorphology. A. Pileipellis diverticulate hyphae. B. Pleurocystidium and basidia. C. Basidiospores. D. Cheilocystidia. Bars: A-C = 10 µm; D = 5 µm.

Habitat & phenology: Subtropical forest, with dominant rhizomorphs scattered or gregarious on fallen or aerial twigs of trees, notably *Quercus*, with rhizomorphs used by birds as nesting material in Mexico; late spring and summer; North American Gulf of Mexico Coastal Plain (Alabama, Florida, Louisiana, Mississippi, Texas).

Pileipellis composed of: 1) pileal hairs (Fig. 24a–c) <80 × 2–4 µm, possibly erect, becoming apically subcapitulate, minutely ornamented; 2) repent diverticulate-ornamented hyphae (Figs 23a,25), 2.5–5.5 µm diam,

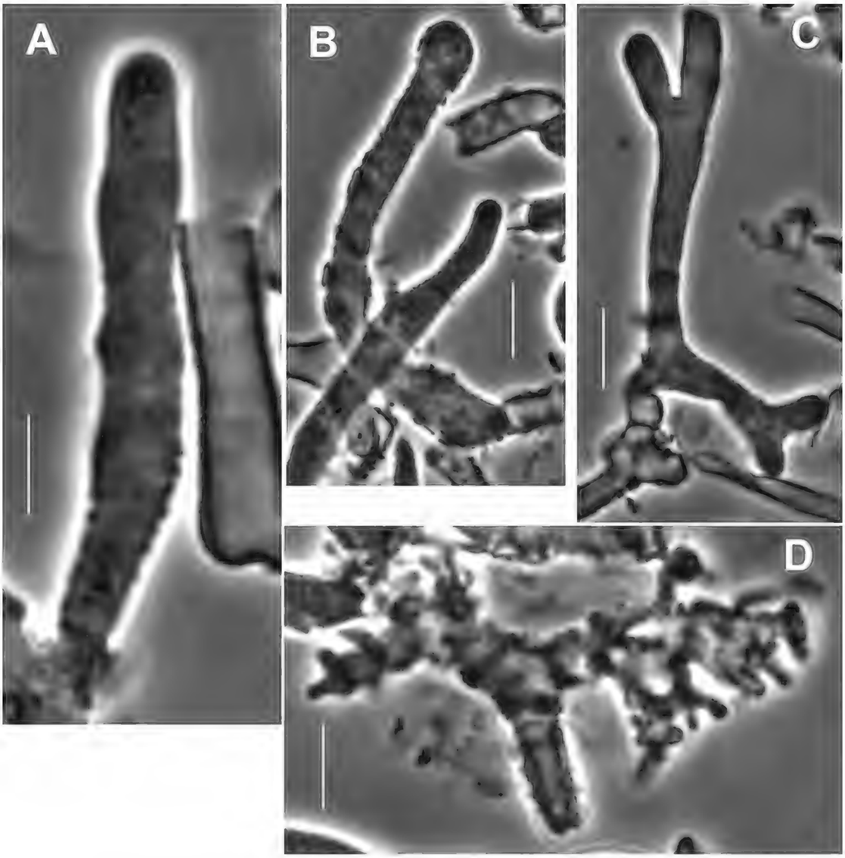

Fig. 24. *Pseudomarasmius nidus-avis* (TENN-F-054912). Micromorphology. A–C. Pileal hairs. D. Broom cell-like pileipellis hyphal terminus. Bars = 10 µm.

thick-walled and diverticulate hyphae termini (Figs 24d,25); diverticula 1–3 × 1–1.5 µm, conical, slightly dextrinoid (fide César & al. 2018); clamp connections absent; 3) tightly interwoven, repent hyphae 2.5–6 µm diam, thick-walled (wall <1 µm thick), ornamented with annular deposits c. 0.5 µm thick (Fig. 26a,b); 4) repent hyphae 2–4.5 µm diam, thick-walled (wall <1 µm thick) with individual slime sheath. Pileus trama composed of interwoven hyphae 2.5–7.5 µm diam, weakly dextrinoid (fide César & al. 2018), individually strongly gelatinized (wall <2.5 µm thick, hyaline), implicitly ornamented with flake-like deposits (seen as carried by individual slime sheath; Fig. 26c,d); clamp connections absent. Lamellar trama loosely

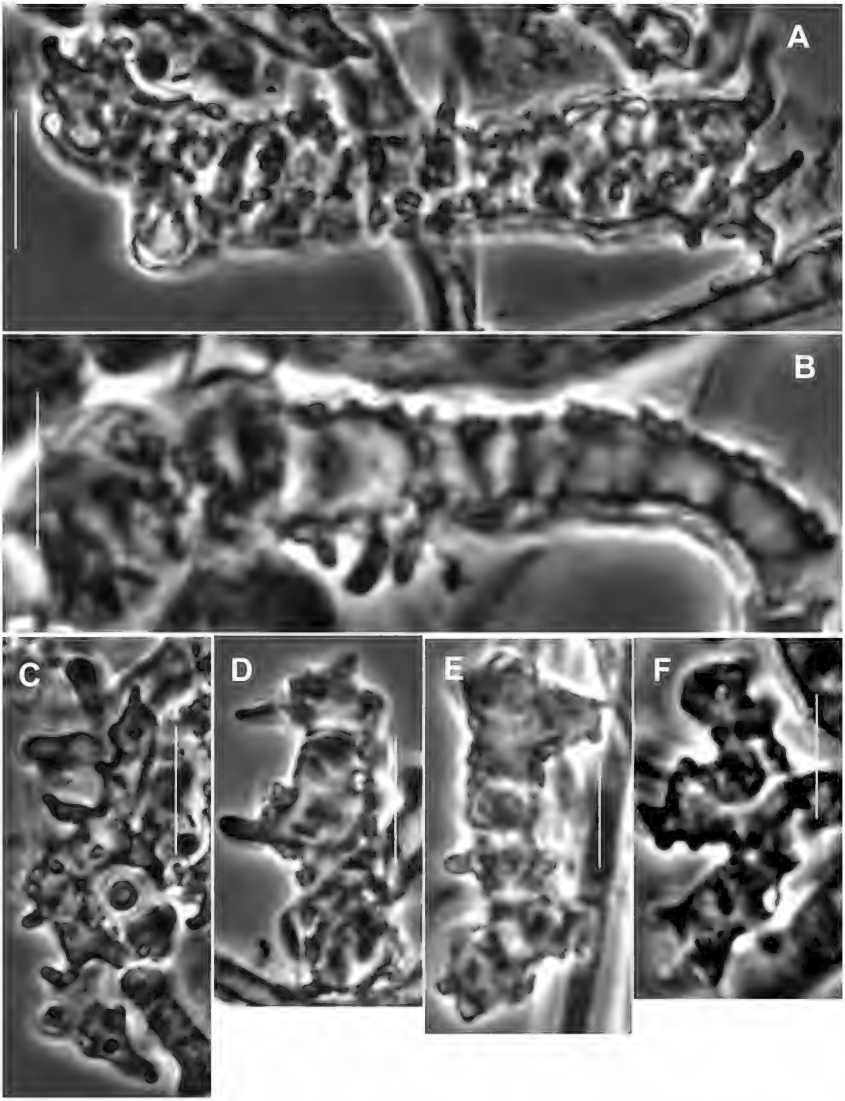

Fig. 25. *Pseudomarasmius nidus-avis* [FLAS-F-60891]. Pileipellis diverticulate hyphae. Compare with Figs 38–40 (*Ps. pallidocephalus*). Bars = 10 µm.

interwoven; hyphae 2–3.5 µm diam, firm-walled, hardly gelatinizing, not easily disarticulated, inamyloid to weakly dextrinoid (fide César & al. 2018); clamp connections absent. Pleurocystidia (Fig. 23b, 27) common, 24–29

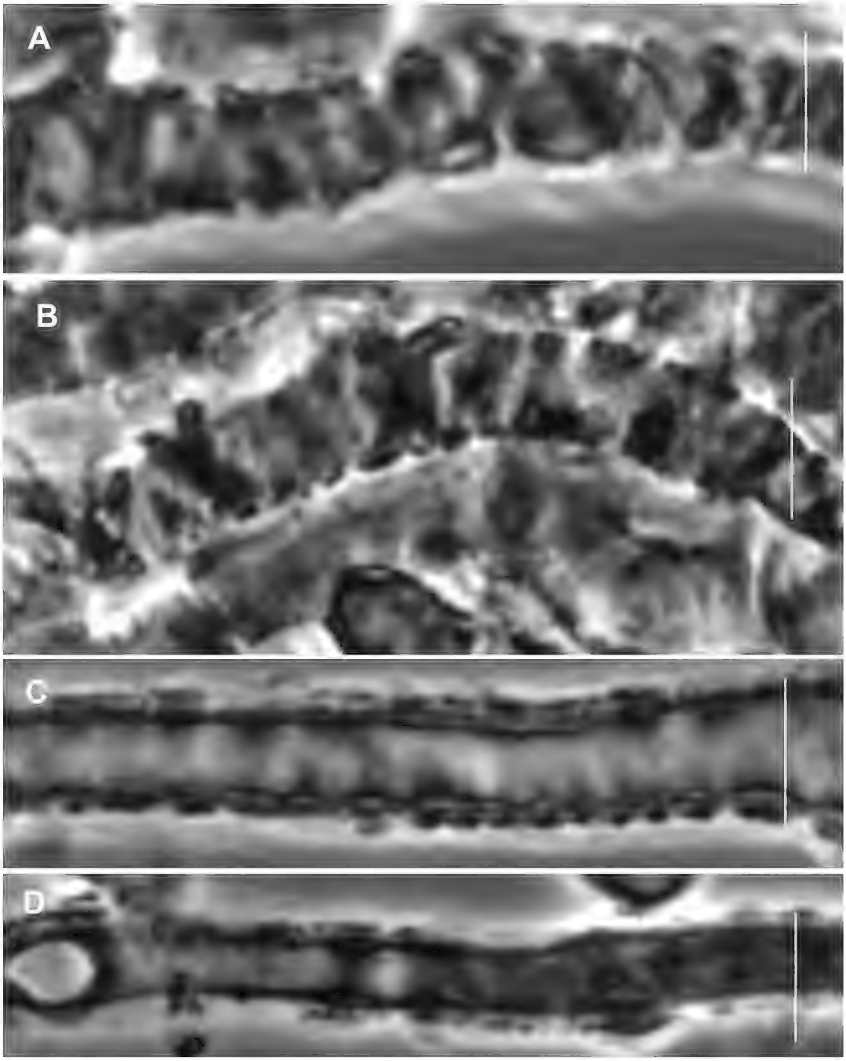

Fig. 26. *Pseudomarasmius nidus-avis* [FLAS-F-60891]. Pileipellis hyphae. A. Hyphal encrustation in scabs. B. Annular ornamentation. C,D. Individual slime sheaths. Bars = 10 µm.

× (5–)6–7 µm, fusiform to plump-fusiform, without clamp connections; contents multiguttulate; guttules refringent (PhC). Basidioles (Fig. 28a) clavate becoming subcapitulate, without clamp connections; basidia (Fig. 28b–d) (20–)27–32(–41) × (5–)9–11 µm, clavate to subcapitulate,

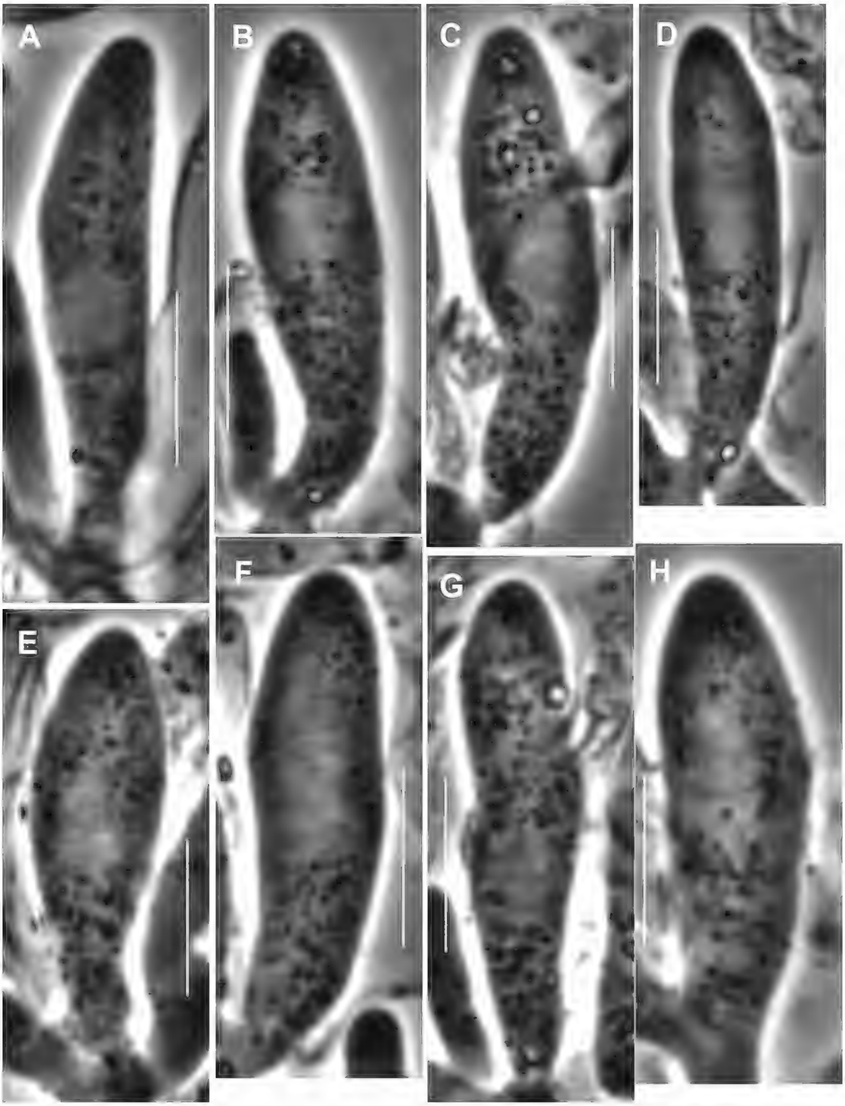

Fig. 27. *Pseudomarasmius nidus-avis* [MES 1477 (FLAS)]. Pleurocystidia. Bars = 10 µm.

(2–)4-sterigmate, without clamp connections; contents multiguttulate; guttules refringent (PhC). Basidiospores (Figs 23c, 28e-h) (7–)8–10.5 × (3–)4–5.5 µm (Q = 1.802.22; Q^m = 1.91; L^m = 9.2 µm), ellipsoid to plump pip-shaped, flattened adaxially, usually somewhat tapered proximally,

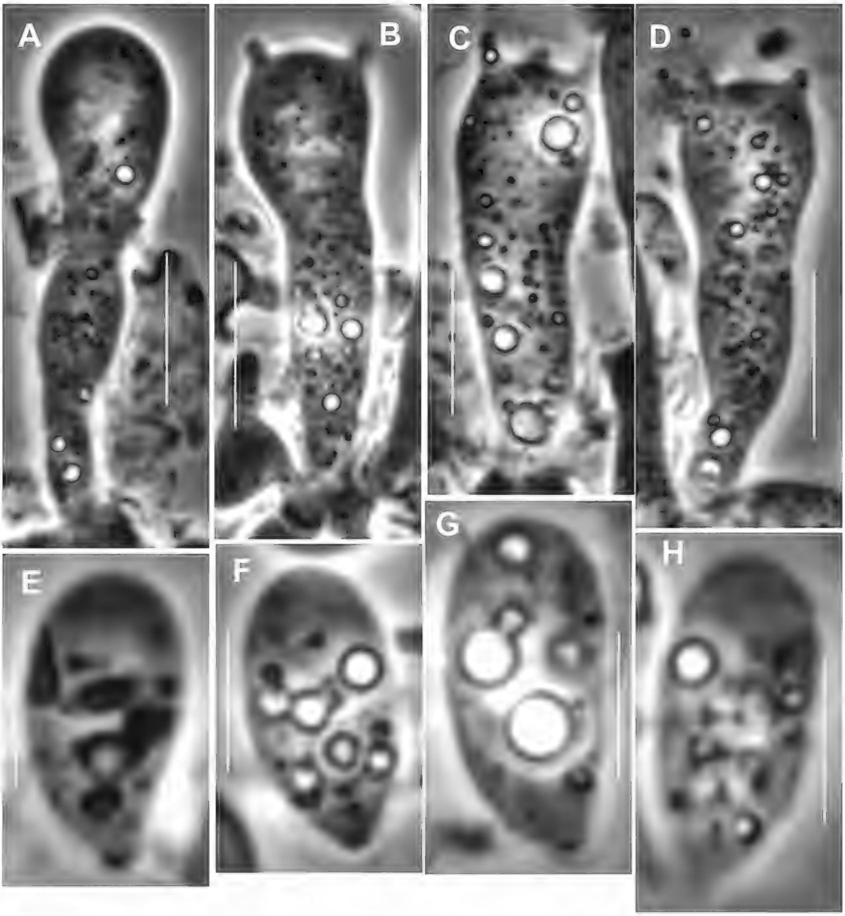

Fig. 28. *Pseudomarasmius nidus-avis* [MES 1477 (FLAS)].
A–D. Basidiole and individual basidia. E–H. Basidiospores. Bars = 10 µm.

hyaline, thin-walled, inamyloid; contents multiguttulate when mature; guttules refringent (PhC). Cheilocystidia (Figs 23d, 29) 20–39 × 3–8 µm, occasional on lamellar edge, hyphal (not inflated), stalked (stalk 2–2.5 µm diam, thin-walled), irregularly lobed and/or branched, without clamp connections; contents homogeneous. Stipe medullary hyphae of two distinct forms: 1) stout hyphae (Fig. 30), 4–15(–30) µm diam, highly refringent (PhC), apparently aseptate or with occasional cloissons d'retret; hyphal walls gelatinizing, occasionally strongly so (wall c. 4.5(–12) µm thick),

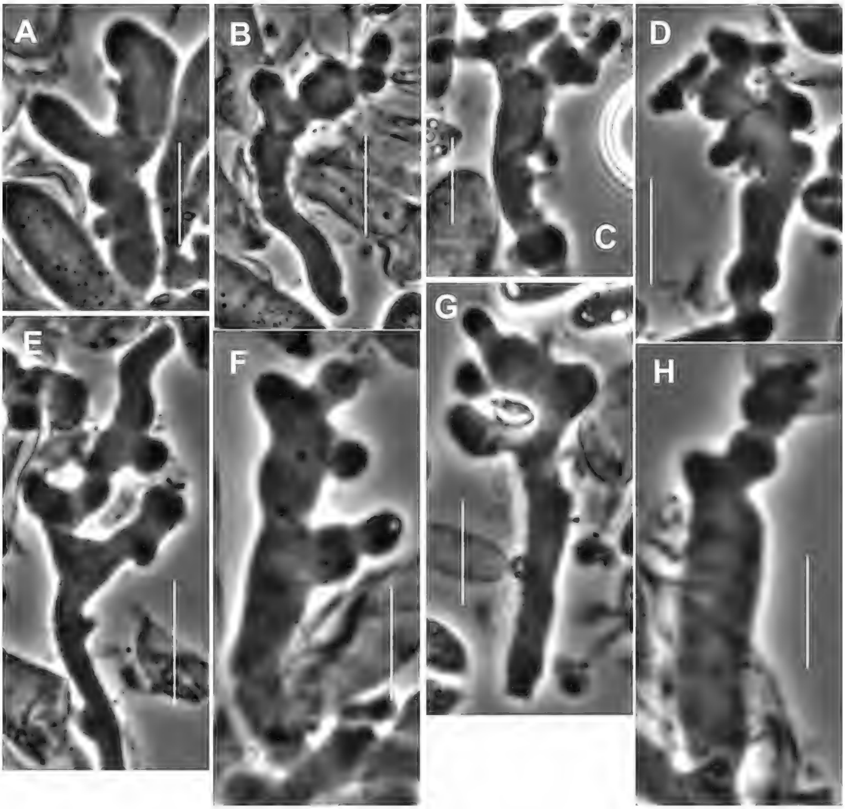

Fig. 29. *Pseudomarasmius nidus-avis* [MES 1477 (FLAS)]. Cheilocystidia. Bars = 10 µm.

often ornamented with flake-like deposits in vague stripes and carried on the outside of the gelatinized sheath; and 2) slender hyphae (Fig. 31), 2–4.5 µm diam, thick-walled (wall c 0.7 µm thick), minutely ornamented, with occasional but conspicuous clamp connections. Stipe cortical hyphae 2.5–7.5 µm diam, repent, strictly parallel, strongly pigmented, thick-walled, minutely encrusted on stipe surface, dextrinoid (red-brown, Melzer's reagent + PhC; reddish brown, Melzer's reagent + BF); pigmented, diverticulate terminal elements 4–19(–21) × 3–4(–5) µm, thin-walled (fide César & al. 2018).

Commentary: A recent paper (César & al. 2018) described *Gymnopus nidus-avis* as clampless (except for scattered clamps in stipe medulla) and with basidiomata arising as side branches from copious, black rhizomorphs.

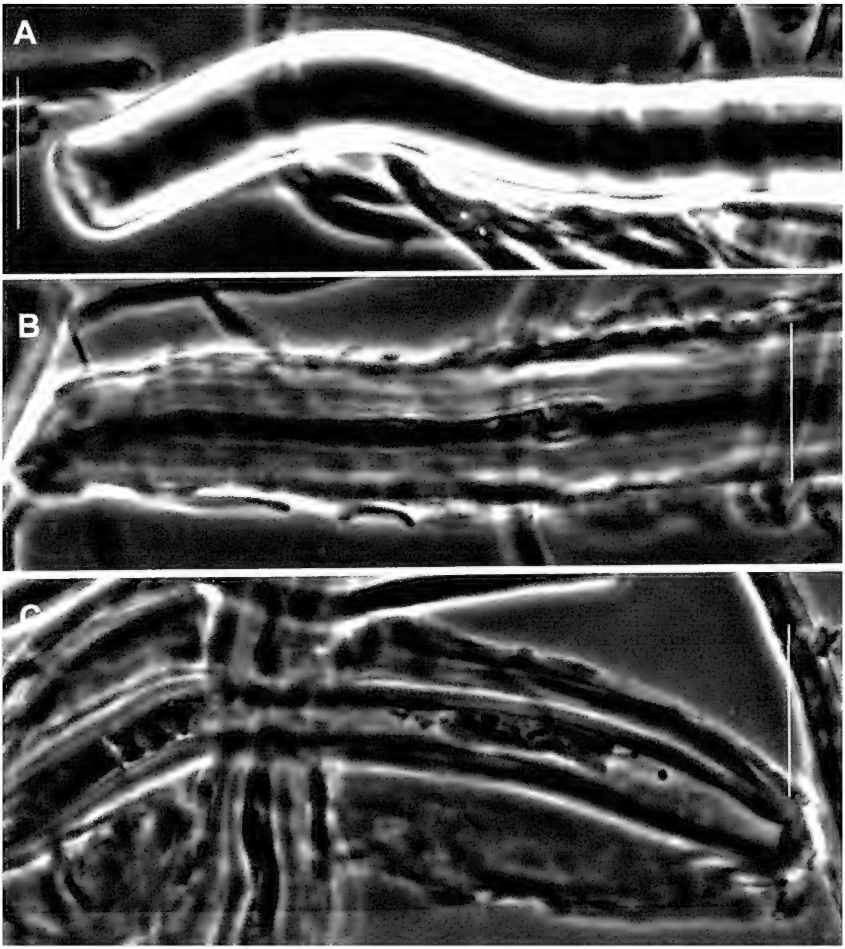

Fig. 30. *Pseudomarasmius nidus-avis* [MES 1477 (FLAS)]. Stout stipe medullary hyphae. A Non-gelatinized hypha. B. Flake-like ornamentation on thin slime sheath. C. Maximum gelatinization. Bars = 10 µm.

ITS sequences from *G. nidus-avis* were intermixed with sequences deposited (by our lab) in GenBank as *Marasmius brevipes*. Independent discovery that voucher collections of these collections of putative *M. brevipes* were clampless confirmed the paraphyletic placement of putative *M. brevipes*. Typical *Marasmius brevipes* (Desjardin & Petersen 1989b) has been transferred to *Gymnopus* (as *G. neobrevipes*; see Petersen & Hughes 2019). Proposal of *G. nidus-avis* including several ITS sequences provides a name for the

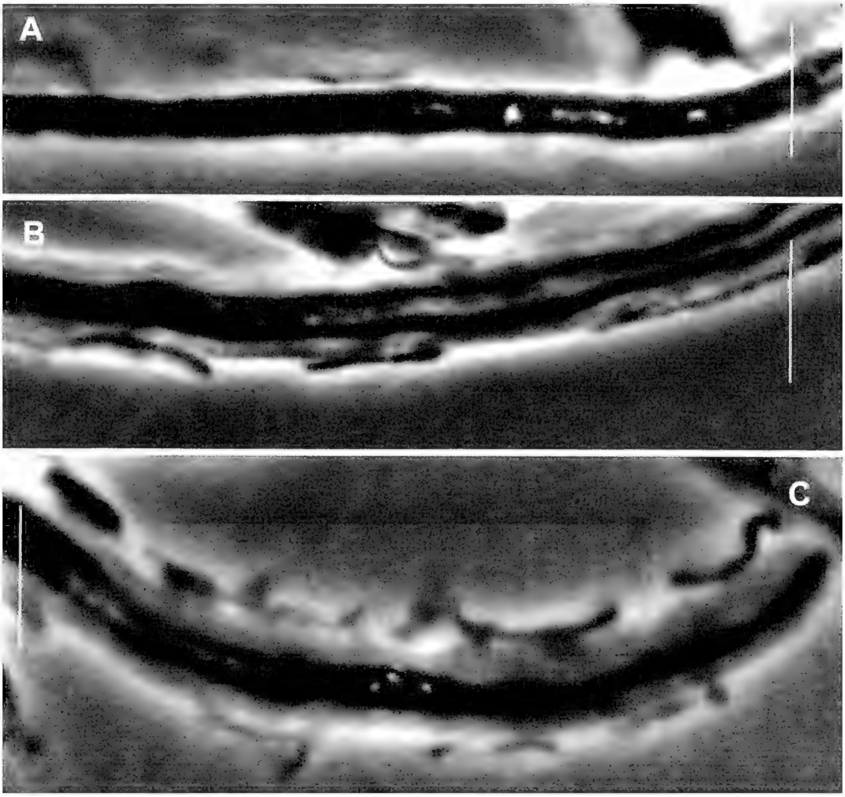

Fig. 31. *Pseudomarasmius nidus-avis* [MES 1477 (FLAS)]. Slender stipe medullary hyphae. A. Non-gelatinized hypha. B. Flake-like ornamentation on thin slime sheath. C. Maximum gelatinization plus ornamentation. Bars = 10 µm.

non-typical collections of putative *M. brevipes*. Inherent is a significantly widened distribution for *G. nidus-avis* from subtropical Mexico to the North American Gulf Coast.

A few specimens at FLAS (variously labelled as unidentified or as "aff. *M. crinis-equi*") lack basidiomata but exhibit rhizomorphs of the *G. nidus-avis* morphology (black, smooth, very slender).

Murrill (1915) proposed *Polymarasmius* for basidiomata which arise as branches of rhizomorphs but noted: "…lamellae adnate to a collar…." *Polymarasmius* was typified by *Marasmius multiceps* Berk. & M.A. Curtis from Cuba, with the other two species from Belize and Jamaica. Such a diagnosis seems to fit *M. crinis-equi* of *Marasmius* subsect. *Sicciformes,* which is known from the subtropics of the New World.

Specimens consulted: **MEXICO. Veracruz, Municipality of Xalapa**, Santuario del Bosque de Niebla, Instituto de Ecología A.C., 1343 m a.s.l., 18 May 2006, Bandala 4052; 7 July 2016, César 41; 10 Aug 2016, Ramos 682 (all at XAL).

Specimens examined: **UNITED STATES. Alabama, Mobile Co.**, Univ. South Alabama, main campus, VII.2014, coll. unknown, det. J.L. Mata, TFB 14607 (TENN-F-69310). **Florida, Alachua Co.**, Gainesville, Possum Creek Park, 20.IV.2016, coll. M.E. Smith ["On suppressed oak understory, fruiting from elevated branches."] MES1477 (FLAS-F-62667: as *Marasmius "crinis-equi"*); Gainesville, Sweetwater Reserve, 28.VII.18, coll. M.E. Smith, MES3139 (FLAS-F-62668 as *Marasmius "crinis-equi")*; Gainesville, Rock Creek neighborhood, 1.V.2015, coll. M.E. Smith, MES 884 (FLAS-F-62666; as *Marasmius "crinis-equi"*); **Putnam Co.**, Ordway-Swisher Biological Station, near boat ramp of Lake Suggs, 14.VI.2017, coll. R. Healy & al., FLAS-F-60891 as *Marasmius* cf. *brevipes.* **Louisiana, East Feliciana Parish**, St. Francisville, James John Audubon Historic Site, 30°47.84′N 91°18.43′W, 22.V.1997, coll. RHP, TFB 9087 (TENN-F-054912). **Mississippi, Harrison Co.**, Red Creek Wildlife Management Area, 30°40′35″N 88°54′02″W, 11.VII.2014, coll. KWH, TFB 14498 (TENN-F-069189). **Texas, Orange Co.**, Vidor, Virginia Lane, 30°09.24′N 94°00.66W 26.VI.1976, coll. D.P. Lewis, det. D.E. Desjardin (as *M. brevipes*), Lewis 276 (TENN-F-047666).

Pseudomarasmius obscurus R.H. Petersen, sp. nov. Figs 32–35

IF 555731

Differs from *Gymnopus pyracanthoides* by its 1) marasmioid basidiomata (stipe slender, black; pileus small, gray, dry); 2) habit on dead, sclerophyllous *Quercus* leaves; 3) copious and obvious resupinate rhizomorphs; and 4) lack of clamp connections.

Type: Costa Rica, Prov. San José, Jardin de Dota, 3.5 km W of Interamerican Highway at El Empalme, 9°4′52″N 83°58′28″W, 15.VI.1995, coll. RHP, TFB 7812 (**Holotype,** TENN-F-053787).

Etymology: Referring to the difficulty in observing microscopic structures.

Basidiomata (Fig. 32a) diminutive, very slender. Pileus 25 mm broad, convex at all ages, becoming essentially applanate with downturned margin by maturity, more or less unicolorous when dry, matte; disc mouse gray; outward to margin "tilleul buff" (7B2), not at all striate, scalloped. Lamellae adnexed to free, thickish, <1 mm broad, seceding in drying to appear pseudocollariate when dried, total lamellae 23–28, through lamellae 13–14, off-white; lamellulae in one rank, often ridge-like. Stipe 11–22 × 0.3–0.6 mm, insititious, terete when fresh becoming channeled on drying, appearing superficially glabrous-shining but under magnification (40×) minutely pruinose upward, apically dark brown, extending into pseudocollarium, very dark brown downward to black-brown lower portion. Rhizomorphs common, often resupinate on leaf surface and there anchored by lateral brownish ciliatiform mycelium,

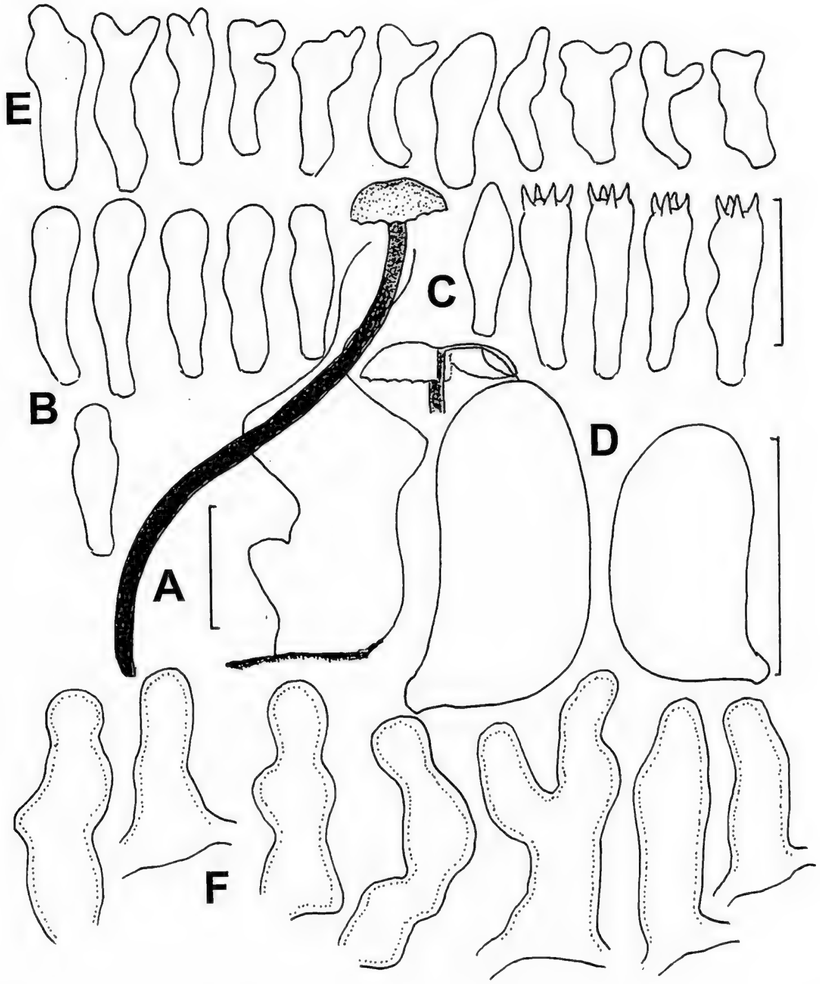

Fig. 32. *Pseudomarasmius obscurus* (TENN-F-053787). A. Basidioma and rhizomorphs with inset showing lamellar attachment. B. Basidioles. C. Pleurocystidium and basidia; D. Basidiospores. E. Cheilocystidia. F. Caulocystidia. Scale bars: A = 5 mm; B,C,E,F. = 20 µm; D = 5 µm.

≤25 mm long where erect, occasionally producing a stellate growth form, very slender (0.1–0.3 mm diam), glabrous-shining, black, curly, frequently branched (similar to those of *G. pyracanthoides*; see Petersen & Hughes 2016).

Distribution & phenology: At present known from a single collection; Costa Rica. Fruiting on sclerophyllous *Quercus* litter with resupinate rhizomorphs; summer.

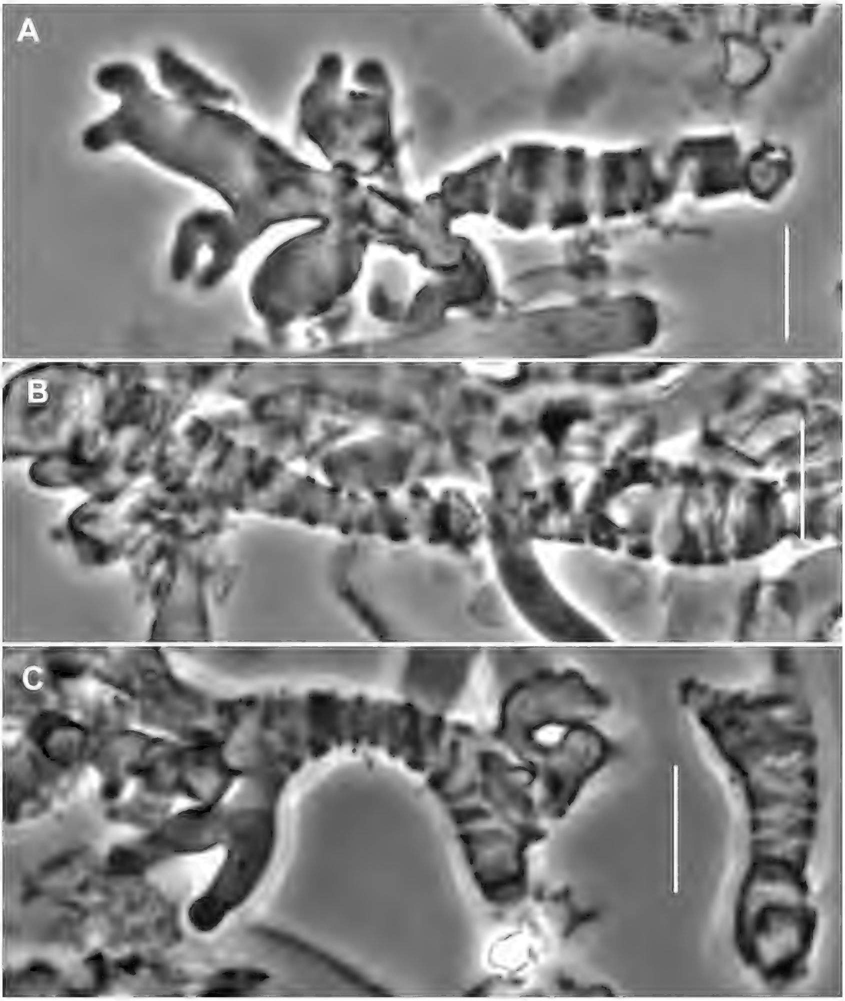

Fig. 33. *Pseudomarasmius obscurus* (TENN-F-053787).
Encrusted hyphae of pileipellis. Scale bar = 10 µm.

Pileipellis composed of two elements: 1) a tangle of free-form, broadly diverticulate hyphae (Fig. 34), 3.5–8 µm diam, thin-walled, variously lobate to subsetulose, often septate, without clamp connections; and 2) strongly encrusted hyphae (Fig. 33) 3–7 µm diam, firm- to thick-walled (wall c. 0.7 µm thick, hyaline); crust material in bands or rings with profile calluses c. 1 µm

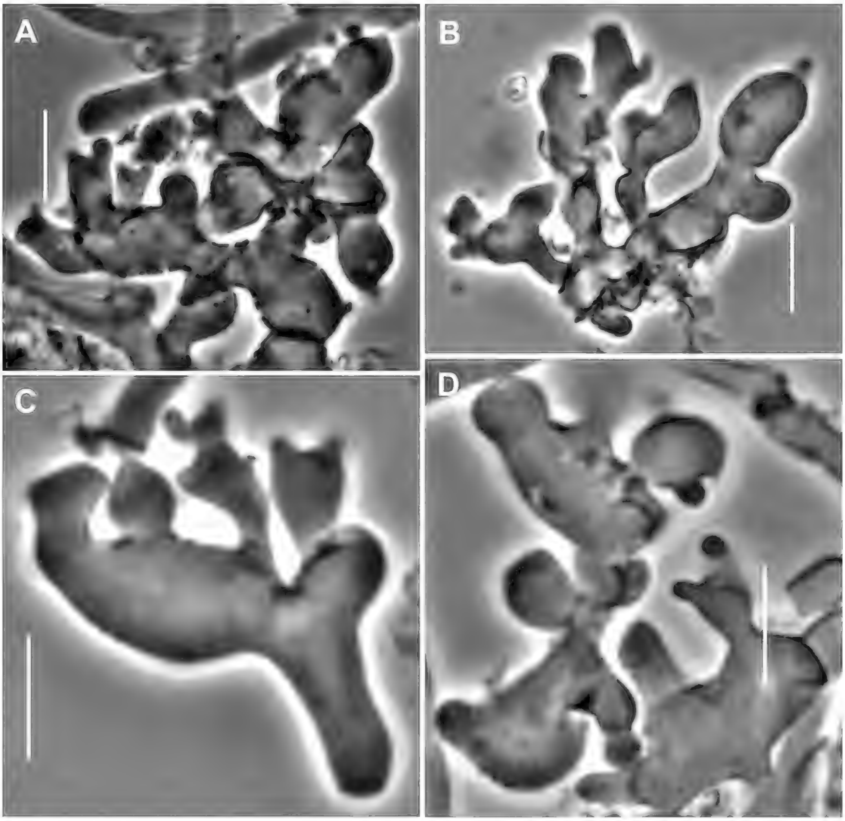

Fig. 34. *Pseudomarasmius obscurus* (TENN-F-037987).
Swollen diverticulate hyphae of pileipellis. Scale bars: 10 µm.

thick. Pleurocystidial structures (Fig. 32c) obscure, 20–28 × 6–8 µm, cylindrical to fusiform, hyaline, thin-walled, without clamp connections. Basidioles (Fig. 32B) clavate to subampulliform; basidia (Fig. 32c) 20–30 × 6–8 µm, clavate to subcapitulate, 4-sterigmate, without clamp connections. Basidiospores (Fig. 32d) 5.5–7 × 3–3.5 µm ($Q = 1.71–2.33$; $Q^m = 1.90$; $L^m = 6.25$ µm), ellipsoid to slightly reniform, variable between tapered proximally and not so, thin-walled, smooth, inamyloid. Cheilocystidia (Fig. 32e) very obscure, 16–25 × 3–8 µm, cylindrical to clavate, often furcate or lobate, thin-walled, hyaline, without clamp connections. Stipe medullary hyphae 4–7 µm diam, thick-walled (wall <1 µm thick, hyaline to weakly

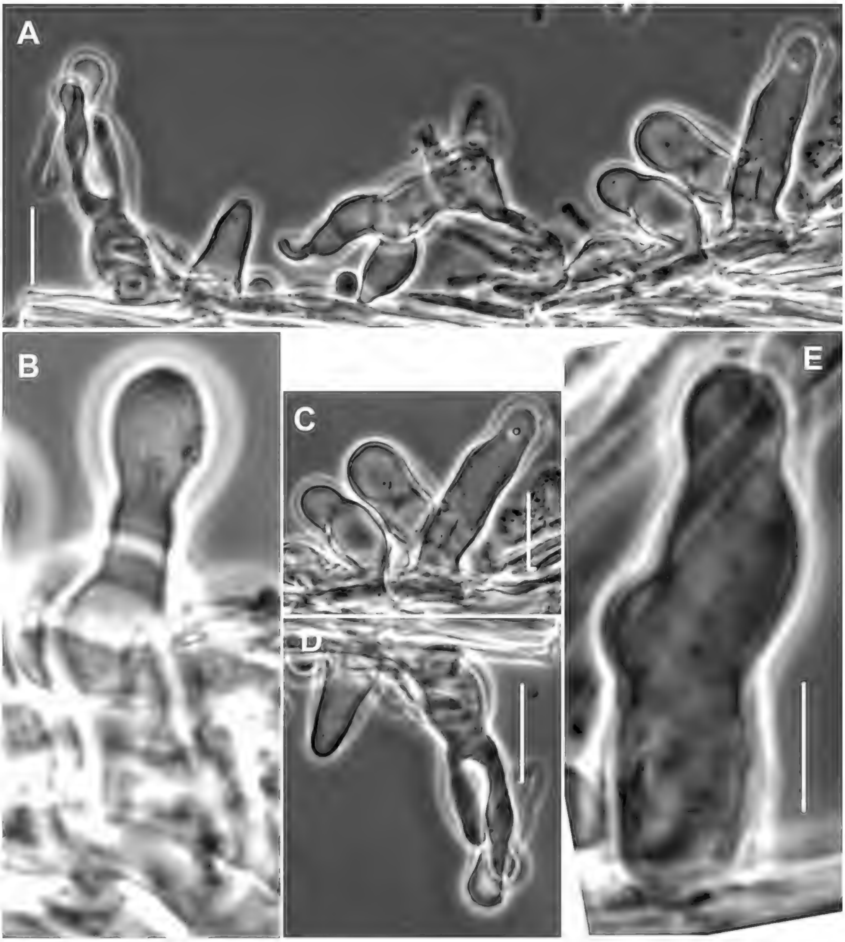

Fig. 35. *Pseudomarasmius obscurus* (TENN-F-053787).
Caulocystidia. Scale bars: 10 µm.

pigmented), strictly parallel, with occasional slender, thin-walled, strangulate-digitate to branched hyphae, without clamp connections. Stipe cortical hyphae 3.5–7.5 µm diam, thick-walled (wall often occluding cell lumen), heavily pigmented, distal on stipe producing densely scattered caulocystidia. Caulocystidia (Figs 32f, 35) limited to distal third of stipe, 22–41 × 8–11 µm, variously shaped from pyramidal to furcate to subampulliform, thick-walled (wall <1.0 µm, hyaline), usually with broader base than apex and usually with narrow hyphal origin.

COMMENTARY: Without DNA sequences, accurate placement of TFB 7812 is problematic, but several morphological characters would suggest *Pseudomarasmius*. Production of resupinate rhizomorphs is similar to *G. pyracanthoides* (Petersen & Hughes 2016), also from Costa Rica, also fruiting on *Quercus* leaves and also without clamp connections. The two differ in pileipellis structure (*G. pyracanthoides* pileipellis an intricate thatch of narrow setulose hyphae) and stipe vesture (*G. pyracanthoides* vesture over entire stipe and caulocystidia longer).

Pseudomarasmius pallidocephalus (Gilliam) R.H. Petersen, **comb. nov.** FIGS 36–42

IF 555745

≡ *Marasmius pallidocephalus* Gilliam, 1975 Mycologia 67: 818.

TYPE: United States, Michigan, Chippewa Co., Gilliam 1165 (MICH!, see below).

Diagnostic characters include: Fruiting on dead spruce and fir needles in North America; 2) basidiomata diminutive, exhibiting a white to off-white pileus and off-black, bristle-like stipe; 3) pileipellis with diverticulate hyphae, free-form hyphal segments and broom cell-like hyphal termini; 4) caulocystidia occasional, ampulliform.

BASIDIOMATA (FIG. 36A, 37) diminutive, marasmioid; ratio of stipe length to pileus breadth high (6–8:1). PILEUS 5–24(–35) mm broad, pulvinate to convex at first, then plano-convex or broadly conic-convex, finally plane to shallowly concave and often subumbonate or umbilicate, dry or subviscid in wet weather, dull opaque, pliant or membranous, reviving, smooth, subtly sulcate-striate, subtuberculate, even or faintly rugulose-striate to disc, minutely velutinous or matted-fibrillose, dark brown in primordia; disc and inner limb brown (7D4) when young, fading to light brownish grey (6C3), soon light yellowish brown (7.3YR/7.0/2.8 Munsell), brown (7E4) to light brown (7D4) to light greyish brown (7D3) overall, by maturity light grayish yellowish brown, light pinkish yellowish brown, light yellowish pink 7A2 ("light pinkish cinnamon"), pale orange yellow, 6A2 ("pale pinkish buff"), light yellowish brown 6B5, 7,3YR/7,0/2.8 (Munsell) ("cinnamon"), dark brown (Maerz & Paul 16A12) moderate 4.7Y/5.2/4.1 (Munsell) yellowish brown, fading to greyish orange (6B2); drying about 5A5 ("ochraceous buff"); outer limb and margin yellowish, at first entire, soon eroded or crenate, white (Maerz & Paul 9B2), pale orange yellow 6A2 ("pale pinkish buff"), 4D2 pale yellowish white to off-white to 7B2 ("tilleul buff"), smooth, brownish grey when young, becoming minutely rugulose-striate, buff in age – overall pallid coloration in age. Pileus trama thin, yellowish white (5.5Y/9.3/1.8 Munsell) to light yellowish brown (7.3YR/7.0/2.8 Munsell).

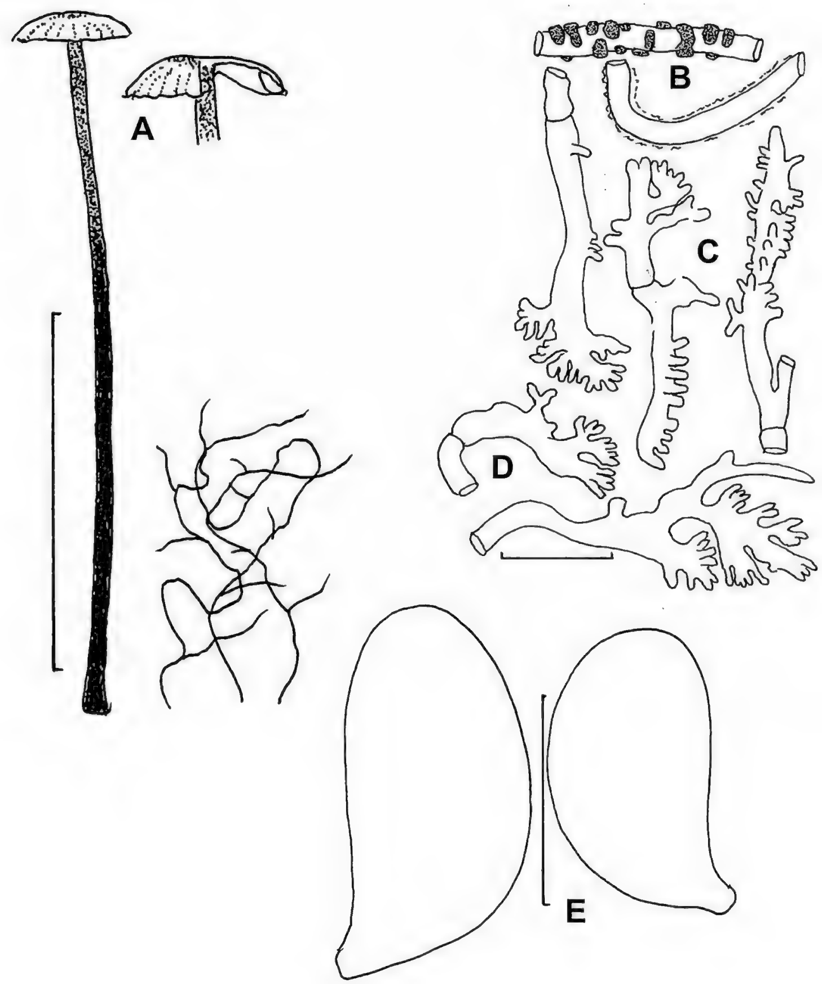

Fig. 36. *Pseudomarasmius pallidocephalus* (TENN-F-063098). A. Basidioma and rhizomorphs. B–D. Pileipellis elements. B. Encrusted hyphal segment and hypha with slime sheath. C. Diverticulate hyphae. D. Diverticulate hyphal termini. E. Basidiospores. Scale bars: A = 20 mm. B–D. = 10 µm. E = 5 µm.

Lamellae narrow (c. 1 mm broad), thin, subdistant, total lamellae = 32–37, through lamellae = 15–17, unequal, adnate at first, becoming adnexed or free to sinuate in age, or sometimes attached to a partial adnate collar, seceding upon drying, pliant, entire or minutely fimbriate, thickish, narrow, straight at first, broader near the stipe in age, not intervenose or obscurely so in age,

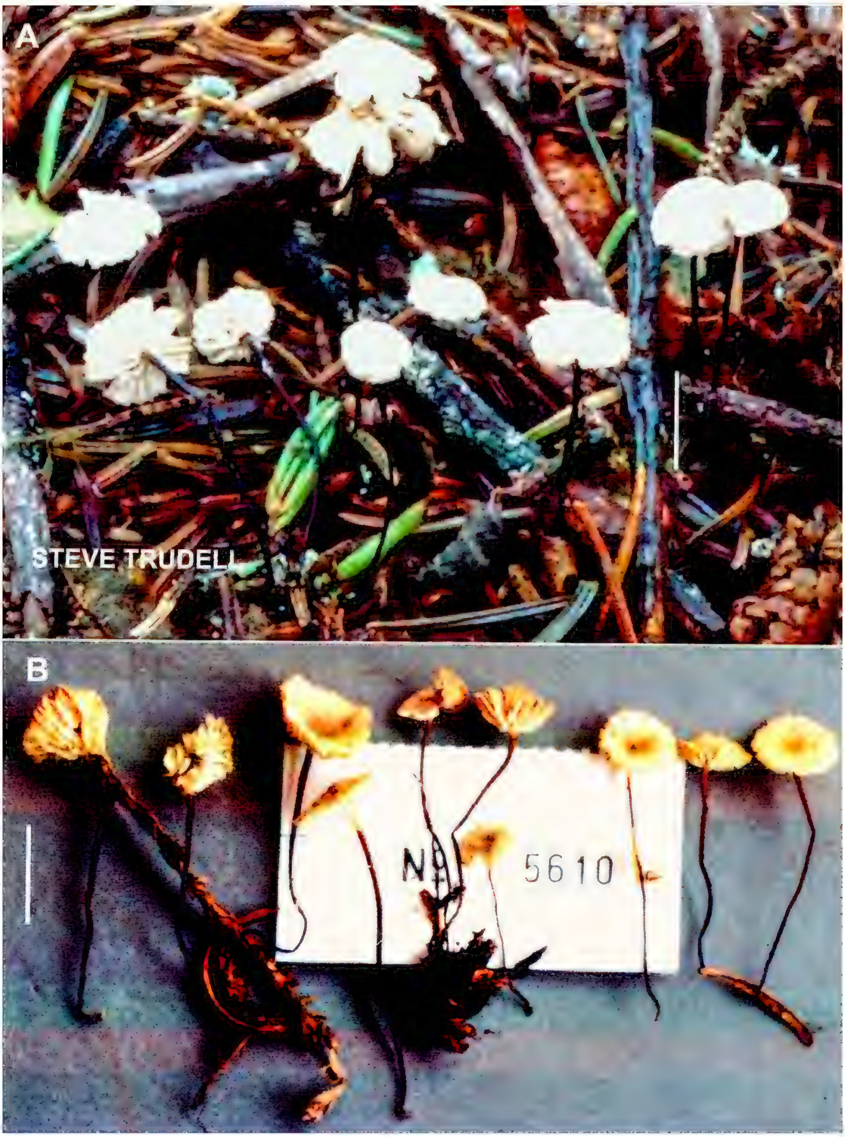

Fig. 37. *Pseudomarasmius pallidocephalus*. Basidiomata. A. Photo from nature (TENN-F-066344). Courtesy Steve Trudell. B. Field-dried basidiomata (TENN-F-052401). Scale bars: 10 mm.

not forked, off-white at first, yellowish white (5.5Y/9.3/1.8 Munsell), pale orange yellow 3A2 ("light buff"), or light yellowish brown (7.3YR/7.0/2.8

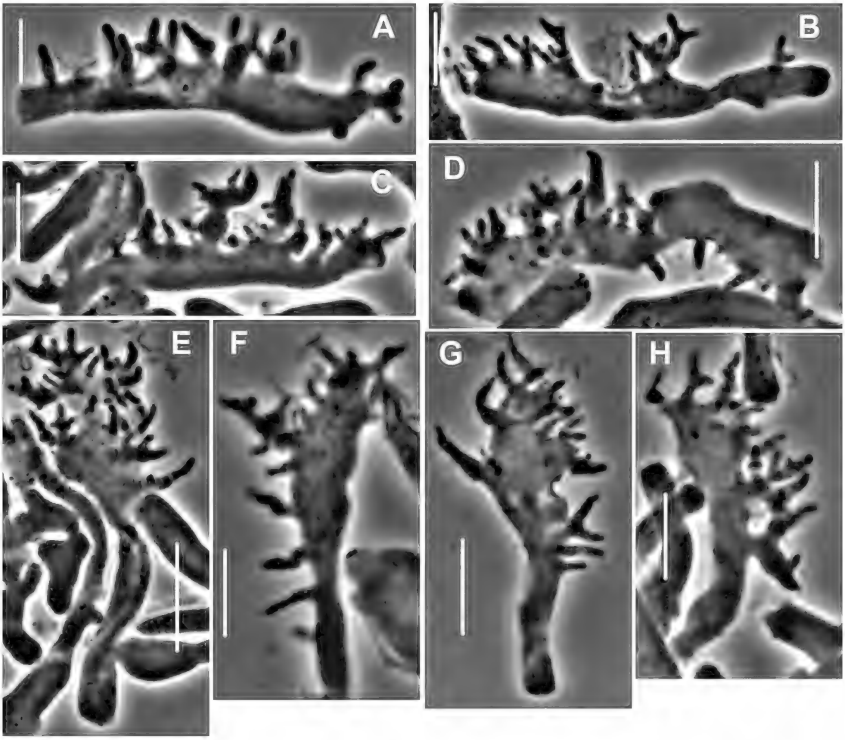

Fig. 38. *Pseudomarasmius pallidocephalus* (TENN-F-020486). Pileipellis elements. A–D. Repent, diverticulate hyphae. E–H. Broom cell-like, diverticulate hyphal termini. Scale bars: 10 µm.

Munsell), soon buff to pale greyish (5A2), buff to pale orange grey (<5B2), soon buff to pale greyish (<5A2), 6A2 ("pale pinkish cinnamon"), ca. 5A4 ("light ochraceous buff"), in age mellowing to 9B2 ("vinaceous buff"), to 6A2 ("pale pinkish cinnamon"), when dried buff to pale orange grey (<5B2); lamellulae in 12 tiers. Stipe 1243 × 0.20.8 mm thick, insititious, central or somewhat eccentric, terete, equal or tapering downward, straight when moist, soon curling and twisting on drying, shining, opaque, hollow, bristle-like but not tough (thin, stiff and easily cut), equal or tapering slightly downward, glabrous; apical 12 mm sometimes whitish-pruinose, more or less concolorous with lamellae ("ochraceous buff"), downward light yellowish brown (7.3YR/7.0/2.8 Munsell) to moderate yellow brown (0.7Y/5.2/4.1 Munsell) or dark reddish brown (10.0R/1.5/1.5 Munsell) to dark brown on the upper half, downward black-brown, brownish grey

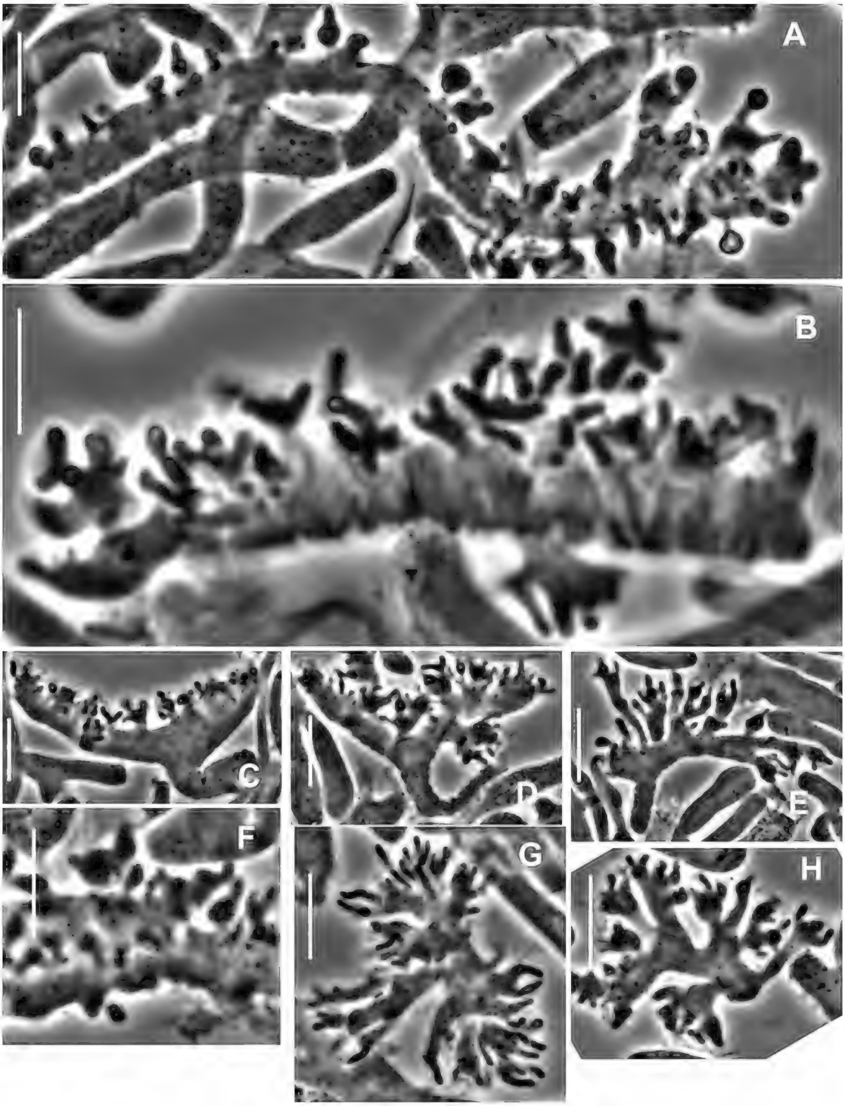

Fig. 39. *Pseudomarasmius pallidocephalus* (MICH 51323). Pileipellis elements. A,B. Repent diverticulate hyphae. C–H. Broom cell-like, diverticulate hyphal termini. Note frequency of di- or trichotomously branched diverticula. Scale bars: 10 µm.

(6C3) to greyish brown (7D3), soon dark brown (7F4-8), 5F8 ("bister"), 6F4 ("fuscous black"), 7F8 ("bone brown"), olive-brown [6E4 ("fuscous"), 2F3

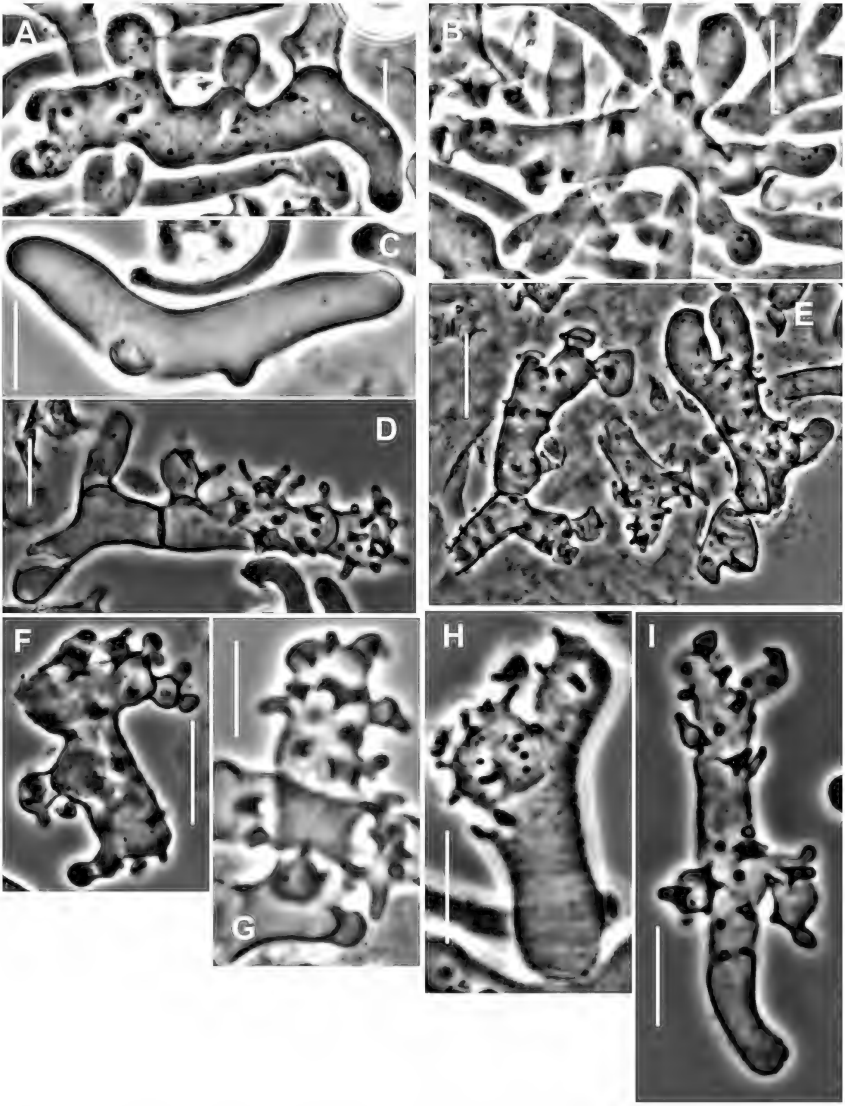

FIG. 40. *Pseudomarasmius pallidocephalus* (WTU-F-8911). Free-form pileipellis elements. A–C. Non-diverticulate individuals. D–I. Diverticulate individuals. Scale bars: 10 µm.

("chaetura black")], never black downward; when dried glabrous-shining, delicately ridged, compressed; basal mycelium absent; sterile stipes absent. RHIZOMORPHS (FIG. 36A) ≤17 × 0.1–0.5 mm, slender, hair-like, scarce to

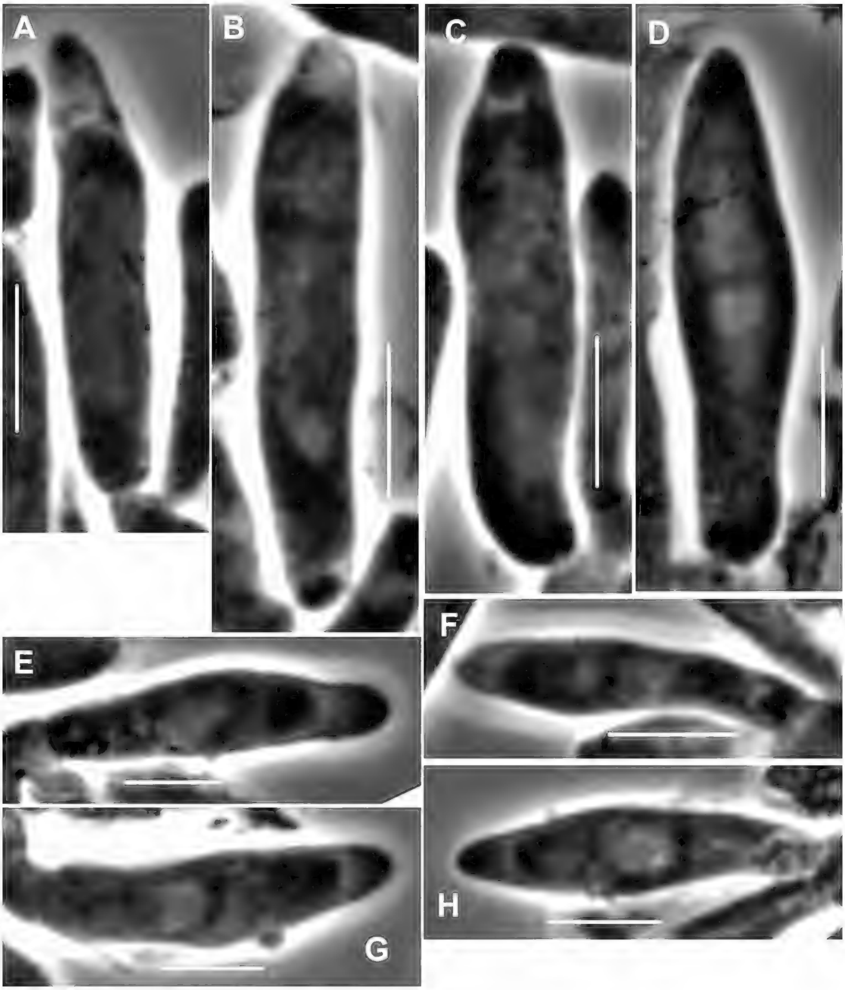

Fig. 41. *Pseudomarasmius pallidocephalus*.
Pleurocystidia (A–D. MICH 51323. E–H. TENN-F-026266).
Note frequent distal, vague partition of contents. Scale bars: 10 µm.

abundant, arising at intervals along the substrate, much branched with spur-branches often long and flagelliform, twisted and curled, sometimes forming a loose tangle. Odor negligible; taste negligible.

Habitat & phenology: Occasional to common in troops on needles and debris of conifers, chiefly *Picea* and *Abies* in spruce-fir forest, rarely on *Thuja* debris: highest elevation of southern Appalachian Mountains, north through

New England into and across the continent to the Pacific Coast temperate rain forest and there accompanied by *Pseudotsuga menziesii*, *Arbutus menziesii*, *Quercus garryana*, *Acer macrophyllum*, and occasionally *Thuja plicata*, with understory of *Alnus*, *Salix*, *Shepherdia;* apparently a mid-summer fungus.

PILEIPELLIS composed of the following elements embedded in a thin slime matrix: 1) repent hyphae 3–7.5 µm diam, firm- to thick-walled (wall c. 0.5 µm thick), hyaline individually, yellowish in mass, coarsely ornamented variously from stripes with plate-like profile calluses to flake-like with the flakes very slightly separated from the hyphal outer wall as though with a very thin slime layer between; 2) scattered free-form hyphal segments (FIG. 40) as in a "*dryophila*-structure," but not articulated into a cutis; 3) repent hyphae (FIGS 36B–D, 38A–D, 39) 4–40 × 4–10 µm, inflated somewhat, with diverticulate, papillate to digitate (often forked) processes, 2–6 × 0.7–3 µm at base, not thick-walled, sub-refringent, sometimes in pairs or dichotomously branched (i.e. "saddle-shaped"), distributed more or less randomly (not unilateral); and 4) broom cell-like termini (FIGS 36C, D, 38E–H, 39C–H, 40D–I) usually arising from lightly encrusted hyphae, stalked (stalk 15–25 × 3.5–5.5 µm), thin-walled, often branched dichotomously and then often divaricate, beset by numerous diverticula; diverticula lobate to conical and sometimes with a combination of forms; clamp connections absent. PILEUS TRAMA loosely interwoven; hyphae 4.5–13 µm diam, firm-walled, without clamp connections, involved in minimal individual slime sheath but not coherent in tissues, occasionally coarsely ornamented with annular incrustation ≤2 µm thick, often ornamented with vague, poorly defined stripes. LAMELLAR TRAMA loosely interwoven; hyphae 2.5–8(–13) µm diam, firm- to thick-walled (wall c. 0.5 µm thick, hyaline), involved in minimal individual slime sheath but not coherent in tissues, occasionally coarsely ornamented with annular incrustation ≤2 µm thick, often ornamented with vague, poorly defined stripes, easily disarticulated; clamp connections absent. PLEUROCYSTIDIA (FIG. 41) 23–33 × 5–8 µm, narrowly fusiform to fusiform with narrowing rounded apex, usually without content partition, without clamp connections; contents homogeneous but with vague central vacuolated area (PhC). Basidioles clavate-subcapitate, clampless; contents vaguely multigranular; BASIDIA (FIG. 42A–D) (20–)25–34 × (4–)5–8(–10) µm, clavate, (2)4-sterigmate, without clamp connections; contents multigranular. BASIDIOSPORES (FIG. 36E) (5–)5.5–7(–9.5) × 3–3.5(–6) µm (Q = 1.30–2.33; Q^m = 1.87; L^m = 6.7 µm), ellipsoid to plump ellipsoid to elongate pip-shaped, flattened adaxially, not tapered proximally, thin-walled, smooth, inamyloid;

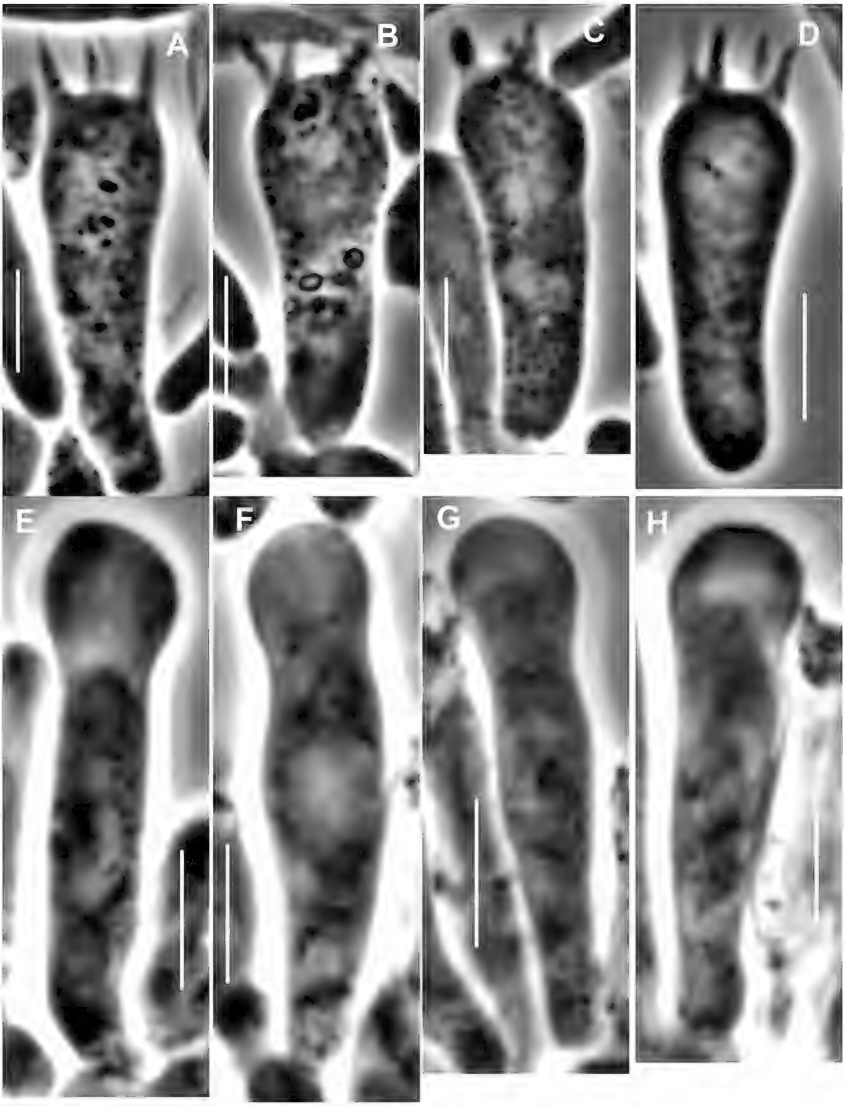

FIG. 42. *Pseudomarasmius pallidocephalus*. Hymenial structures.
A–D. Basidia (MICH 51323). E–H. Cheilocystidia (TENN-F-026266).
Scale bars: 10 µm.

contents homogeneous. CHEILOCYSTIDIA (FIG. 42E–H) scattered, similar to basidioles, 21–30 × 5–8.5 µm, clavate at first, becoming ampulliform by maturity, without clamp connections. STIPE MEDULLARY HYPHAE (FIG. 43)

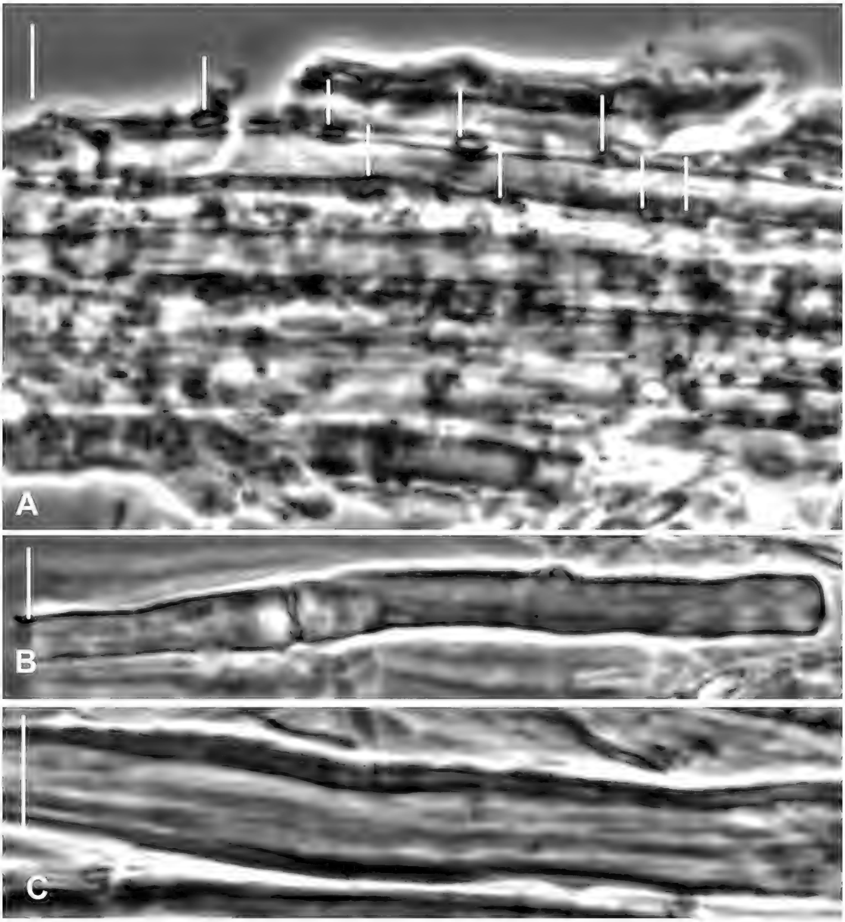

Fig. 43. *Pseudomarasmius pallidocephalus* (TENN-F-056761). Stipe medullary hyphae. A. Outer hyphae, with lines marking hyphal crust depositions. Stipe surface upward in photo. B, C. Individual inner medullary hyphae. B. Notes septum without clamp connection. C. Note wall thickness. Scale bars: 10 µm.

(inner) (2–)3.5–8.5 µm diam, strictly parallel, firm- to thick-walled (wall ≤1.2 µm thick, hyaline), coherent in tissues (i.e. minimal slime matrix), lacking clamp connections; outer medullary hyphae 1–3.5(–7.5) µm, firm- to thick-walled (wall <1 µm thick, hyaline, ornamented with lens-shaped encrustation often appearing pitted). Stipe cortical hyphae moderately to strongly dextrinoid, 3–5.5 µm diam, thick-walled (wall often occluding cell lumen), smooth or covered with heterogeneous slime with inclusions.

COMMENTARY: *Pseudomarasmius pallidocephalus* combines characters seen in other related complexes. Basidiome stature, size, rhizomorphs, and habitat all mimic (or are mimicked by) *Gymnopus* sect. *Androsacei* and/or *G.* sect. *Perforantia*. The minimal slime matrix of the pileipellis and stipe medullary hyphae resemble those of *Gymnopus* sect. *Perforantia*, while dextrinoid stipe cortical tissue is like that of some members of /marasmiellus (ss Wilson & Desjardin (2005). The diverticulate hyphae of pileipellis resemble those of *Mycetinis* (including the inflated cells typical of that genus), not those of *Marasmius* (*siccus*-type) and the free-form hyphal segments of pileipellis are similar to such structures in *Gymnopus* sect. *Levipedes* ("*dryophilus*-structure"). Lack of clamp connections, however, seems quite unusual in related complexes. Several taxa in *Gymnopus* sect. *Androsacei* have been described as clampless, mostly by Singer, and they generally have been found in New- and Old-World tropical forests and none with accompanying molecular phylogenies.

Desjardin (1989) reported *Ps.* (as *Marasmius*) *pallidocephalus* as "one of the more commonly collected, early-fruiting litter-decomposing agarics in the spruce-fir zone of the southern Appalachians." In these spruce-fir forests, it has been and is easily misidentified as *G.* (as *Micromphale*) *perforans*, which usually exhibits a pigmented pileus toward cinnamon or avellaneous and vestured stipe. *Gymnopus androsaceus* is encountered only occasionally.

Pleurocystidia in *P. pallidocephalus* are typical of such structures found widely through gymnopoid/marasmioid fungi. Such structures are fusiform in shape, with narrowly rounded apex, as opposed to clavate to subcapitulate shapes of basidioles. Apparently without taxonomic relevance, pleurocystidial shapes are sometimes accompanied by vaguely partitioned contents. In *Ps. pallidocephalus*, however, such structures are often more broadly rounded apically. Basidioles and basidia, conversely seem to be consistently clavate from an early stage, and with heterogeneous contents (FIG. 42A–D), unlike pleurocystidial structures which remain homogeneous in content. In numerous descriptions (including our publications up to a couple years ago) the structures termed here as pleurocystidia were included under the perceived variability of basidioles.

Gilliam (1975) mentioned clamp connections only once, under pileus tramal hyphae. This observation was erroneous: clamp connections are consistently absent on all basidiomatal hyphae in *Ps. pallidocephalus*. Desjardin (1990) examined cultures of *Ps. pallidocephalus* and reported the absence of clamp connections.

Past experience (Petersen 1978, Petersen & Hughes 2010) has produced some links between absence of clamp connections, 2-spored basidia, and oversize basidiospores indicative of haploid state, together with unexplained sexual compatibility systems. These links seem irrelevant in *Ps. pallidocephalus*, where basidiomata lacking clamp connections normally produce 4-spored basidia. The mating system of this species remains unknown.

Gilliam (1975) seemed intent on separating *Ps.* (as *Marasmius*) *pallidocephalus* from *M. androsaceus,* the often-reported taxon which fruits on similar substrates in Europe and North America. Her concept of *M. androsaceus* was revealed in the concluding lines of her discussion, as fruiting on a "variety of habitats." Not only is this observation understandable given the state of prior literature and the date of her study, but it may have influenced Desjardin's (1989) treatment of *M. androsaceus* in his dissertation, which also drew no attention to clamp connections. Currently, phylogenies indicate that *M. androsaceus* may be split into at least three species: *M. androsaceus* fruiting on conifer debris, plus two which fruit on dead deciduous leaves (Petersen & Hughes, ined.). Other mimics fruit on pine needles [*Gymnopus* (*Micromphale*) *pinophilus* complex; Petersen & Hughes 2016a], cedar twigs and redwood litter [*Gymnopus* (*Micromphale) sequoiae* complex]. In addition to presence/absence of clamp connections, *Ps. pallidocephalus* lacks conspicuous cheilocystidia [only a few ampulliform shapes reminiscent of those of *G. trabzonensis* (Vizzini & al. 2015)] while *G. androsaceus* exhibits common cheilocystidial structures. Finally, Gilliam (1975) reported the lack of "hymenial cystidia" (inclusive of pleuro- and cheilocystidia) in *M. pallidocephalus*, perhaps because pleurocystidia are not conspicuous. Our experience with other taxa indicates that pleurocystidial structures are present.

Rhizomorph presence and activity are arcane in *Ps. pallidocephalus*. Basidiomata are usually formed on dead needles from the previous 1–2 years, but the needle bed on which they are found is usually deeper, with more decayed needles (differing in color and substance) and these decayed needles are held together by tangles of slender, branched, black rhizomorphs. Rhizomorphs at the surface of the needle bed, and therefore accompanying basidiomata, are usually individual, extremely slender, short, and therefore easily overlooked.

Examination of numerous marasmioid specimens from Europe has not revealed a single specimen of *Ps. pallidocephalus*.

Specimens examined: **CANADA, British Columbia, Cariboo Regional District**, Ft. St. James, 54°26′34″N 124°15′04″W, 13.VII.1940, coll. T.T. McCabe, det. J.W. Groves (as *M. androsaceus*), TTM 253 (UC 1319403); **Stikine Region**, Liard River Hotsprings Prov. Park, 59°25′06″N 126°05′27″W, 18.VIII.2000, coll. R. Winder, O. Ceska, det. O. Ceska (as *M. androsaceus*) (UBC F21036); **Metro Vancouver Regional District**, Mt. Seymour Prov. Park, base of chair lift, 49°22′51″N 122°56′24″W, 27.VIII.1973, coll. S.A. Redhead (as *M. androsaceus*) (UBC F8178); **Capital Regional District**,, Saanich Peninsula, Observatory Hill, 48°31′44″N 123°25′19″W, 17.X.2008, coll. O. Ceska (as *M. androsaceus*) (UBC F29843); Observatory Hill, 48°31′44″N 123°25′19″W, 17.X.2008, coll. O. Ceska (as *M. androsaceus*) (UBC F29843); Observatory Hill, 48°51.67′N 123°42.20′W, 28.II.2010, coll. & det. O. Ceska (as *M. androsaceus*), UBC-F24293; **Fraser Valley Regional District**, Manning Prov. Park, Rhododendron Flats, 49°13′N 121°04′W, 11.VI.2006, coll. Paul Kroeger (as *M. androsaceus*), PK 4072 (UBC F17578). **UNITED STATES, Alaska, Fairbanks**, Fairbanks North Star, Ballane Lake Marge, 64°54.82′N 147°42.31′W, 15.VII.2006, coll. G.A. Laursen [as *Marasmius androsaceu*s], GAL 19442a (WTU-F-31851). **Idaho, Bonner Co.**, Priest Lake, Luby Bay, 48°32′50″N 116°55′24″W, 25.IX.1992, coll. RHP (as *M. androsaceus*), TFB 5632 (TENN 52407); **Shoshone Co.**, vic. Wallace, Coeur d'Alene Nat. Forest., 47°30′N 115°53′W, 24.IX.1992, coll. RHP (as *M. androsaceus*), TFB 5610 (TENN 52401); **Maine, Hancock Co.**, rte 182, vic. Mud Pond and Salmon Pond, 44°37′58″N 68°05′14″W, 21.VII.1992, coll. S.A. Gordon, TFB 4987 (TENN 56761). **Michigan, Cheboygan Co.**, vic. Univ. Michigan Biological Station, Hermit Swamp, 45°33′31″N 84°40′43″W, 26.VI.1957, coll. R.L. Shaffer (as *M.* cfr. *androsaceus*), RLS 1291 (MICH 51323); **Chippewa Co.**, Tahquamenon Falls State Park, Lower Falls, 46°36′16″N 85°12′11″W, 22.VII.1971, coll. & det. M. Gilliam (HOLOTYPE), MSG 1165 (MICH 11402, portion only); **Marquette Co.**, Pine Plains, W of Michigamme State Forest, "Triple A" road, 46°31′14″N 88°03′14″W, 15.VII.1970, coll. J.F. Ammirati & S.J. Mazzer, det. M. Gilliam (as *M. pallidocephalus*), SJM 4479 (MICH 51322). **Minnesota, Clearwater Co.**, Itasca State Park, 9.VIII.1968, coll. M.G. Weaver (as *Marasmius* sp.), det. M. Gilliam (as *M. pallidocephalus*), MGW 1621 (MICH 175913). **New York, Franklin Co.**, Paul Smith's, NEMF pre-foray trip no. 1, Hazel Pond Rd., 44°28.89′N 74°16.50′W, 11.VIII.2011, coll. A.S. Methven, TFB 13933 (TENN 65829); **North Carolina, Swain Co.**, vic. Bryson City, GSMNP, Spruce-Fir Nature Trail, 35°34′02″N 83°28′54″W, 28.VIII.2009, coll. RHP (as *M. androsaceus*), TFB 13664 (TENN 63098); 8.VI.1991, coll. S.A. Gordon, TFB 3623 (TENN 50742); 28.VIII.2009, coll. RHP, TFB 13664 (TENN 63098); vic. Bryson City, GSMNP, Clingman's Dome, 35°33′40″N 83°29′45″W, 10.IX.1985, coll. D.E. Desjardin, DED 3412 (TENN 54660); 35°33′47″N 83°29′55″W, 27.IV.1954, coll. A.H. Smith & L.R. Hesler (TENN 021343). **Tennessee, Blount Co.**, GSMNP, Appalachian Trail vic Clingman's Dome, near old Indian Gap road, 28.V.2011, coll. Steve Trudell, SAT-11-11-179-05 (TENN 66344); **Sevier Co.**, GSMNP, Indian Gap, Appalachian Trail, 35°36′35″N 83°26′19″W, 29.V.2004, coll. RHP (as *M. androsaceus*), TFB 11778 (TENN 59896); 36°36′35″N 83°26′19″W, 13.VII.2004, coll. S.C. McCleneghan & E.B. Lickey, TFB 11970 (TENN 59975); Old Indian Gap Road, 28.VI.1986, coll. D.E. Desjardin, DED 3691 (TENN 54667); 19.VII.1988, coll. D.E. Desjardin, DED 4615 (TENN 54650); 11.VI.1986, coll. D.E. Desjardin, DED 3581 (TENN 54646); **Washington, Jefferson Co.**, Olympic

National Park, Enchanted Valley, 47.6675°N 123.3939°W, coll. J.W. Lennox (as *M. androsaceus*), JWL 511 (WTU-F-8911); **Lewis Co.**, Skate Creek Rd., between Horse Creek and milepost 17, 2.X.1993, coll. RHP (as *M. androsaceus*), TFB 5698 (TENN 53475).

Pseudomarasmius patagonianus R.H. Petersen, **sp. nov.** Figs 44–48

IF 555733

Differs from *Pseudomarasmius nidus-avis* by its 1) slender rhizomorphs that are present but not dominant; 2) basidiomata arising as branches of rhizomorphs or from rotting leaves; 3) pileipellis elements usually semi-gelatinized; and 4) distribution in southern South America (Chilé).

Type: Chilé, Chiloé, Isla Grande de Chiloé, Ancud, 41°52′18″S 73°49′06″W, 9.V.1995, coll. RHP, TFB 7363 (**Holotype,** TENN-F-054432).

Etymology: Referring to the Patagonian origin of the collections.

Basidiomata (Fig. 44a) marasmielloid, short-stipitate, similar to those of *Ps. nidus-avis*. Pileus ≤11 mm broad, campanulate with downturned margin becoming more or less applanate, often abruptly umbilicate, subtly striate, somewhat pulvinate, matte, from uniformly 6C6 ("tawny") to disc 6B5 ("cinnamon") when young, paler in age; outward "pinkish buff" (6A3) to off-white. Lamellae adnate to shortly decurrent, distant, ranging from well-defined to reduced, usually as shallow (<1 mm broad) pleats, ≤20 total folds, 5–8 through folds, 5A2 ("pale cinnamon pink") to off-white (now 4A2 "pale ochraceous buff"). Stipe 2–8 × 1.5–2.5 mm, terete, equal, straight to usually strongly curved, black, upward glabrous shining, downward minutely pruinose, non-insititious with minimal basal tuft. Rhizomorphs rare, slender, black, of unknown length. Odor and taste negligible.

Habitat & phenology: A poorly understood taxon, erumpent on woody substrate, noted as "on hardwood boughs;" Chilean winter.

Pileipellis comprising the following: 1) at pileus margin, repent diverticulate hyphae 2.5–5.5 µm diam, firm-walled, not gelatinized, hyaline; diverticula stout, ≤7 × 1–2.5 µm at base, gnarled-pyramidal, often dichotomous; 2) at pileus margin, diverticulate hyphal termini (hardly broom cell-like) (Fig. 45), resembling repent diverticulate hyphae, perhaps sometimes erect; 3) over disc and limb, occasional pileal hairs ≤75 × 3–4.5 µm, cylindrical, subtly capitulate, arising as an erect branch of the repent hypha; 4) unorganized hyphae 3–6.5 µm diam, thin-walled, variously ornamented (Fig. 46) with crust material often coarsely in scabs <2 µm thick (Fig. 46b), often appearing annular (Fig. 46a,c), easily disarticulated; 5) hyphae 2.5–4.5 µm, not easily crushed, thick-walled (wall ≤0.7 µm thick),

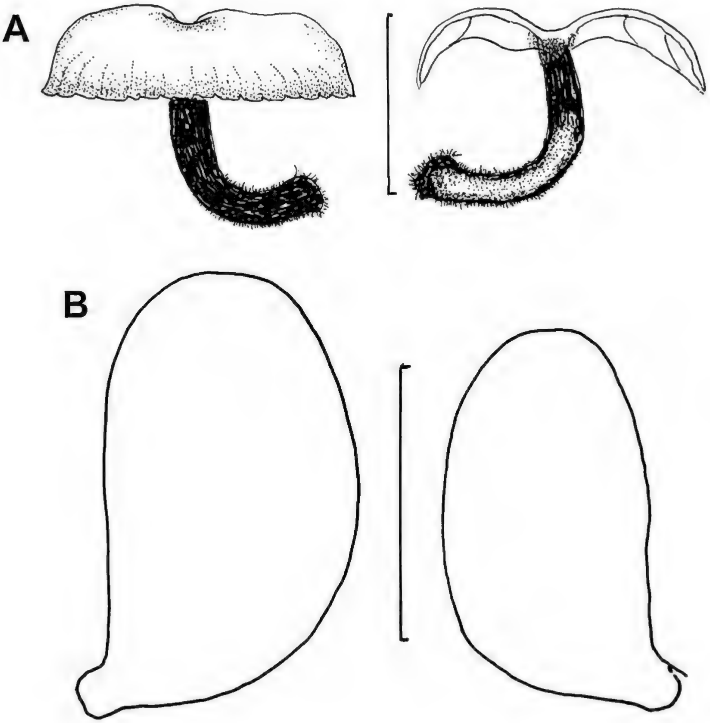

FIG. 44. *Pseudomarasmius patagonianus* (TENN-F-054432, holotype).
A. Basidiomata (left) habit; (right) longitudinal section.
B. Basidiospores. Scale bars: A = 5 mm; B = 5 µm. TFB 7363

often with thin individual slime sheath with flake-like ornamentation (FIG. 46D). Diverticulate hyphae or hyphal termini not observed over disc or limb. Lamellar trama loosely interwoven; hyphae 2–5.5 µm diam, firm- to thick-walled (wall ≤ 1 µm thick), often gelatinizing or with individual thin slime sheath, without clamp connections. PLEUROCYSTIDIA (FIG. 47) uncommon or poorly defined, 22–25 × 5–6 µm, fusiform, without clamp connections. BASIDIA (FIG. 48) 28–37 ×10–12 µm, clavate, (2–)4-sterigmate, without clamp connections; contents heterogeneous when mature, emptying but not collapsing ("husking") when effete. BASIDIOSPORES (FIG.44B) 9–9.5 × 4–5 µm (Q = 1.60–2.25; E^m = 2.07), ellipsoid, thin-walled, not tapered proximally, inamyloid. CHEILOCYSTIDIA absent or undifferentiated. STIPE MEDULLARY

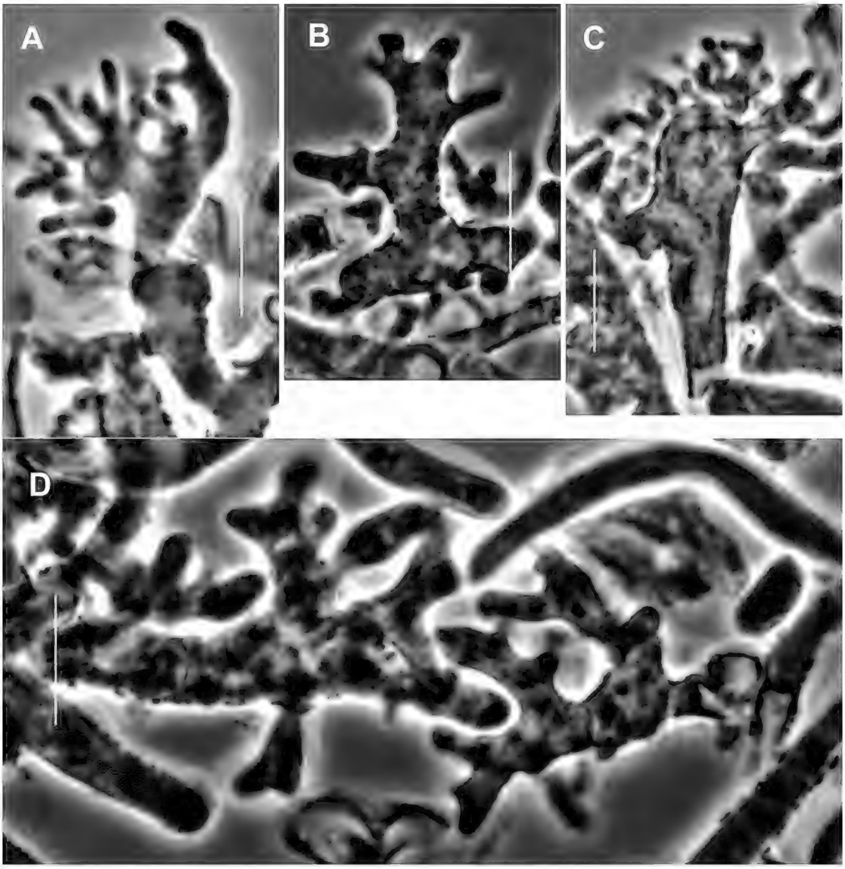

Fig. 45. *Pseudomarasmius patagonianus* (TENN-F-054432, holotype). Pileipellis diverticulate hyphal termini. Scale bars: 10 µm.

hyphae 2.5–5 µm diam, thick-walled (wall ≤1 µm thick), strictly parallel in slime matrix, hyaline, without clamp connections. Stipe cortical hyphae 3–5 µm diam, thick-walled, repent in thin slime matrix, roughened outward, without clamp connections, weakly dextrinoid (reddish tan Melzer's reagent + BF; reddish brown Melzer's reagent + PhC). Caulocystidia ≤65 × 3.5–5 µm, cylindrical, firm-walled, gnarled and often with rudimentary lobes, hyaline singly, dull brown in mass, without clamp connections.

Commentary: Collection TFB7363 (TENN-F-054432) comprises several basidiomata on hardwood substrate. TENN-F-054424, collected in the same

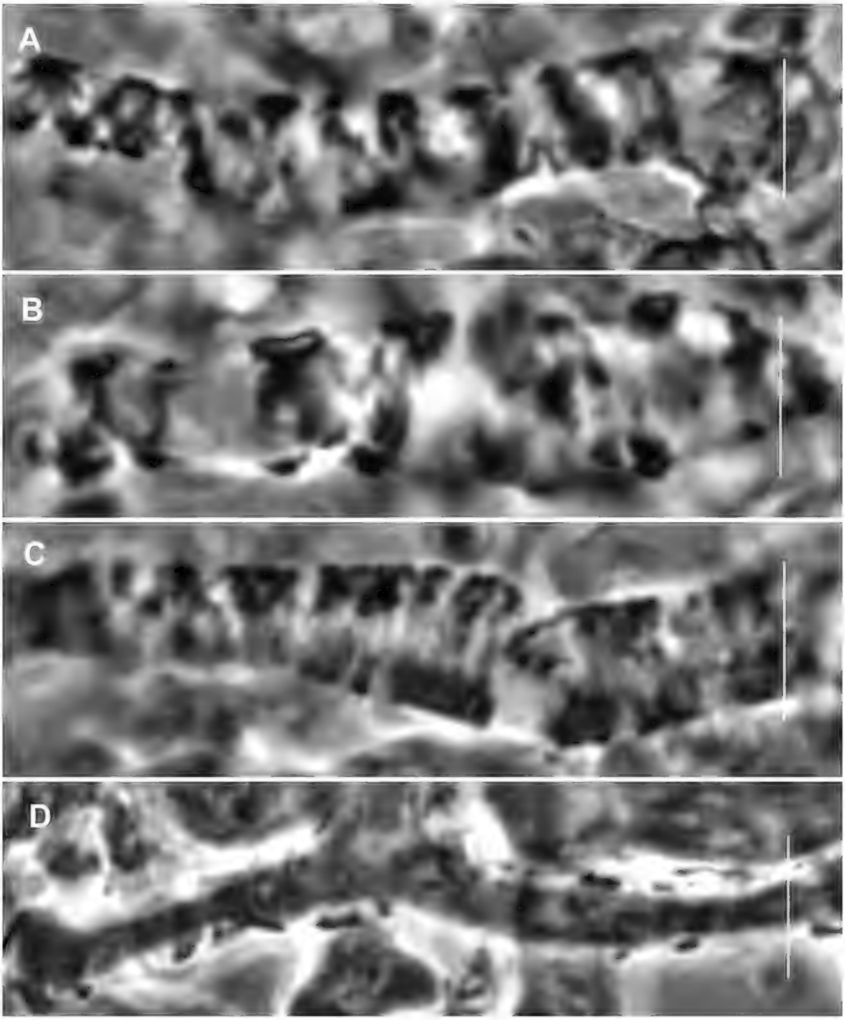

Fig. 46. *Pseudomarasmius patagonianus* (TENN-F-054432, holotype). Pileipellis hyphae. A, B. Encrusted hyphae. A, C. Ornamentation in stripes. B. Ornamentation of scabs -2 µm thick. D. Hypha with individual slime sheath and flake-like encrustation. Scale bars: 10 µm.

location at the same time, is a mixed collection composed of several mycenoid basidiomata and a single marasmielloid basidiome. The ITS-based sequence deposited in GenBank (KY352649; MF978330, rbp2) derived under this accession number must have come from the latter basidiome which is

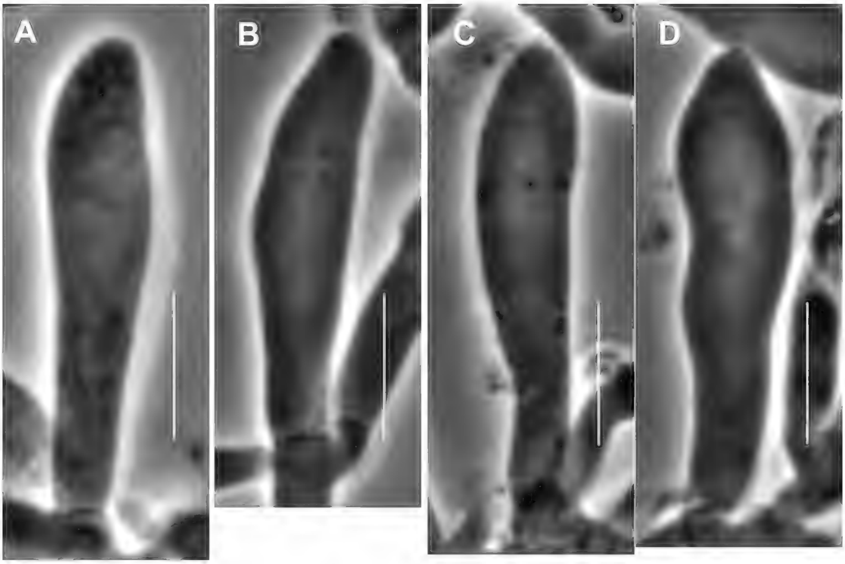

Fig. 47. *Pseudomarasmius patagonianus* (TENN-F-054432, holotype). Pleurocystidia. Scale bars: 10 µm.

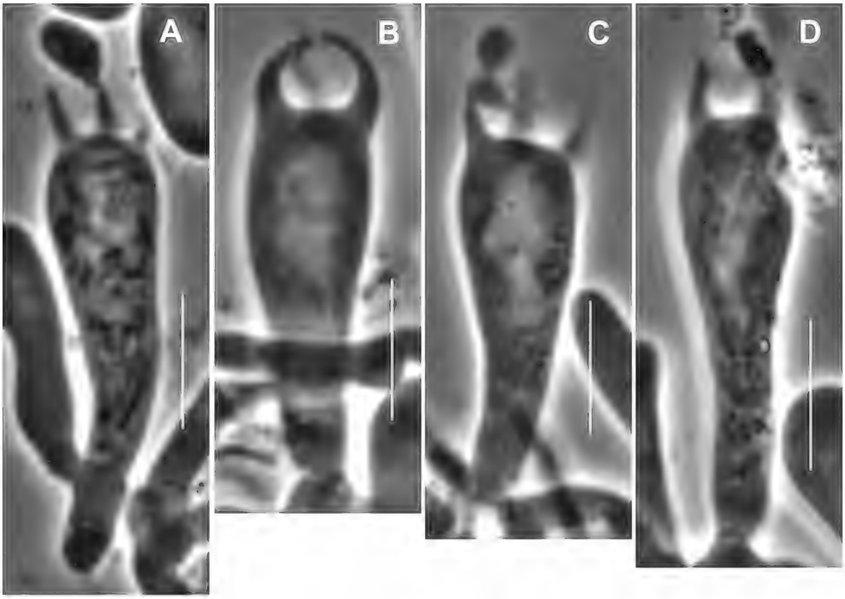

Fig. 48. *Pseudomarasmius patagonianus* (TENN-F-054432, holotype). Basidia. Scale bars: 10 µm.

morphologically identical to basidiomata in TFB7363: the sequence places the collection in *Pseudomarasmius* and the single basidiome matches the generic diagnosis. The basidiome has been segregated within the specimen.

As surveys of herbarium material and phylogenetic analysis of such collections are processed, there appears to be a convergent, relatively common basidiome architecture generally regarded as "marasmielloid," in which basidiomata conform to the following: 1) pileus small, rarely exceeding 15 mm broad, with thin, tough consistency; 2) lamellae usually distant, often reduced and with no anastomoses; 3) stipe central, usually strongly curved, rarely exceeding 10 × 2 mm, black or nearly so, usually glabrous, 4) fruiting on woody substrate often in vertical position; and 5) rhizomorphs usually present and sometimes dominant, slender, black. This architecture might be epitomized by *Gymnopus neobrevipes* (≡ *Marasmius brevipes*), almost indistinguishable from *Ps. nidus-avis* and *Ps. patagonianus* but distinguishable by presence of clamp connections, dominant rhizomorphs, more temperate distribution and unique ITS sequence.

ADDITIONAL SPECIMEN EXAMINED: **CHILÉ**, **CHILOÉ**, **Isla Grande de Chiloé**, 20 km E Aucud, 41°53′10″S 73°38′52″W, 9.VI.1995, coll. RHP, TFB 7364 (TENN-F-054424).

Pseudomarasmius quercophiloides R.H. Petersen, **sp. nov.** FIGS 49–59

IF 555732

Differs from *Gymnopus quercophilus* by its 1) lack of clamp connections; 2) abundant rhizomorphs that are resupinate on sclerophyllous leaves; 3) sulcate-striate pileus with low umbo; and 4) distribution in interior or subtropical China.

TYPE: China, Yunnan Prov., Anning Pref., grounds of Southwest Forestry University, 25°03′51″N 102°45′16″E, 10.VIII.1990, coll. RHP, Q. Wu, Li, TFB 3162 (**Holotype**, TENN-F-049177).

ETYMOLOGY: Resemblance to *Marasmius quercophilus* Pouzar.

BASIDIOMATA (Figs. 49A, 50) diminutive. PILEUS (FIG. 49B) 25 mm broad, downturned, sulcate-striate with small umbo, matte, "vinaceous buff" (9B2). LAMELLAE (FIG. 49B) not collariate, 19–26 total lamellae, 8–11 through lamellae, shallow (<1 mm broad), thick with rounded edge, not marginate, "tilleul buff" (7B2) to "pinkish buff" (6A3). STIPE 8–14 × 0.6–0.9 mm, terete, dull brown apically and there minutely decorated with hyaline caulocystidia, downward appearing glabrous-shining but microscopically pruinose, black, insititious. Rhizomorphs plentiful, resupinate on sclerophyllous hardwood leaves (FIG. 51), dark copper color with minute fringe of ochraceous rust color, rarely becoming aerial but then never pileate.

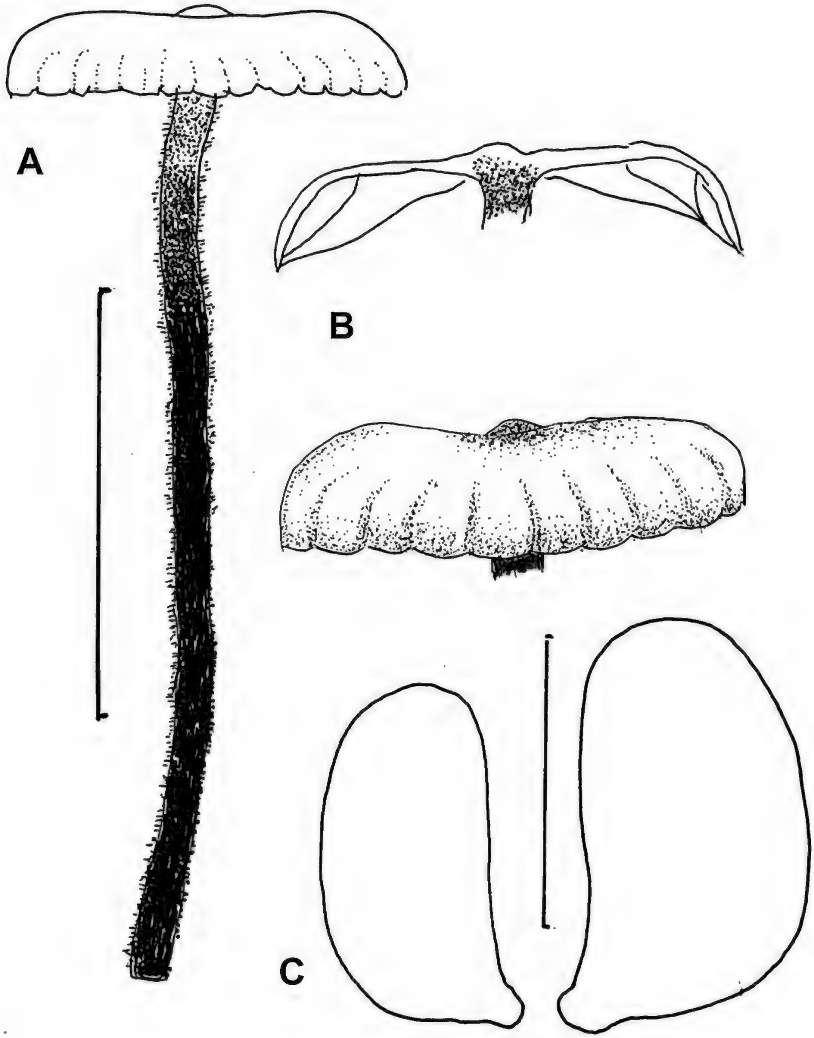

Fig. 49. *Pseudomarasmius quercophiloides* (TENN-F-049179, holotype). A. Basidioma. B. Pileus, exterior + cross-section. C. Basidiospores. Scale bars: A, B = 5 mm; C = 5 µm.

Distribution & phenology: On at least *Castanopsis* leaves in southwestern, subtropical China; summer.

Pileipellis composed of three hyphal types with no evidence of gelatinization: 1) repent hyphae (Fig. 52a) 3–6.5 µm diam, thin-walled,

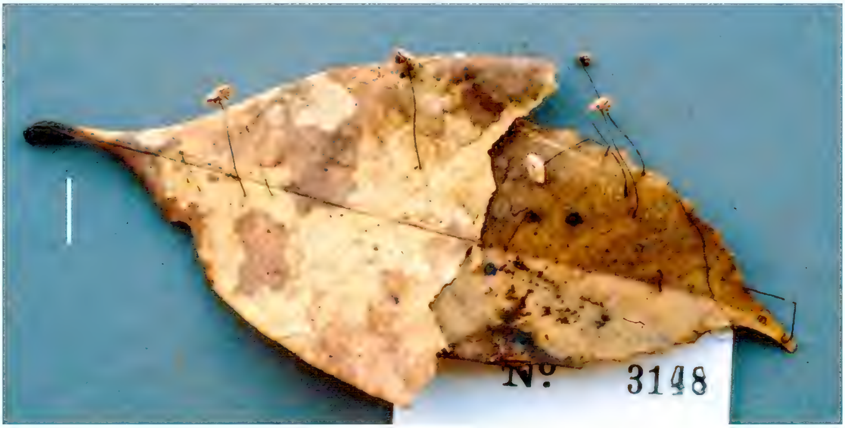

Fig. 50. *Pseudomarasmius quercophiloides* (TENN-F-049179, holotype). Basidiomata on leaf surface. Scale bar = 10 mm.

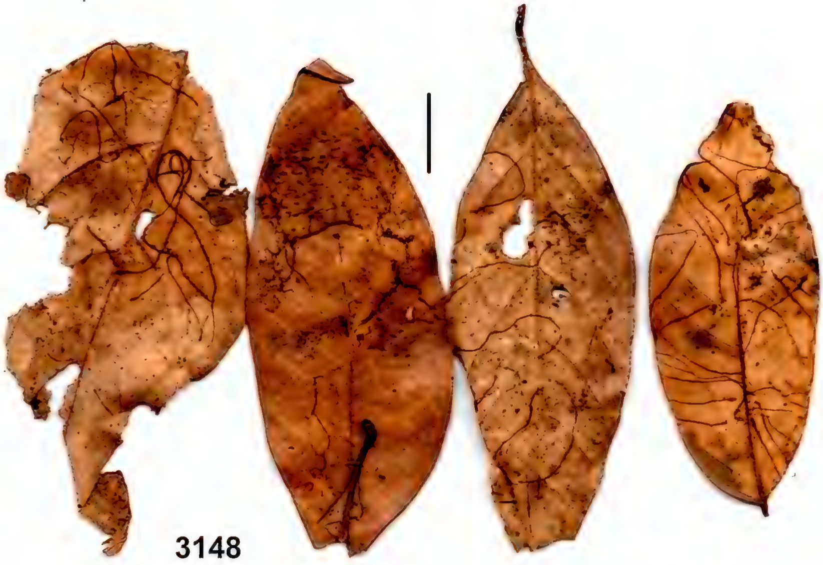

Fig. 51. *Pseudomarasmius quercophiloides* (TENN-F-049179, holotype). Resupinate rhizomorphs on sclerophyllous leaves. Scale bar = 10 mm.

encrusted in scabs not in annular or striped configuration; profile scabs ≤1 µm thick; clamp connections not observed; 2) diverticulate hyphae (Fig. 52b,c) 3–6.5 µm diam, thin-walled, beset with numerous diverticula;

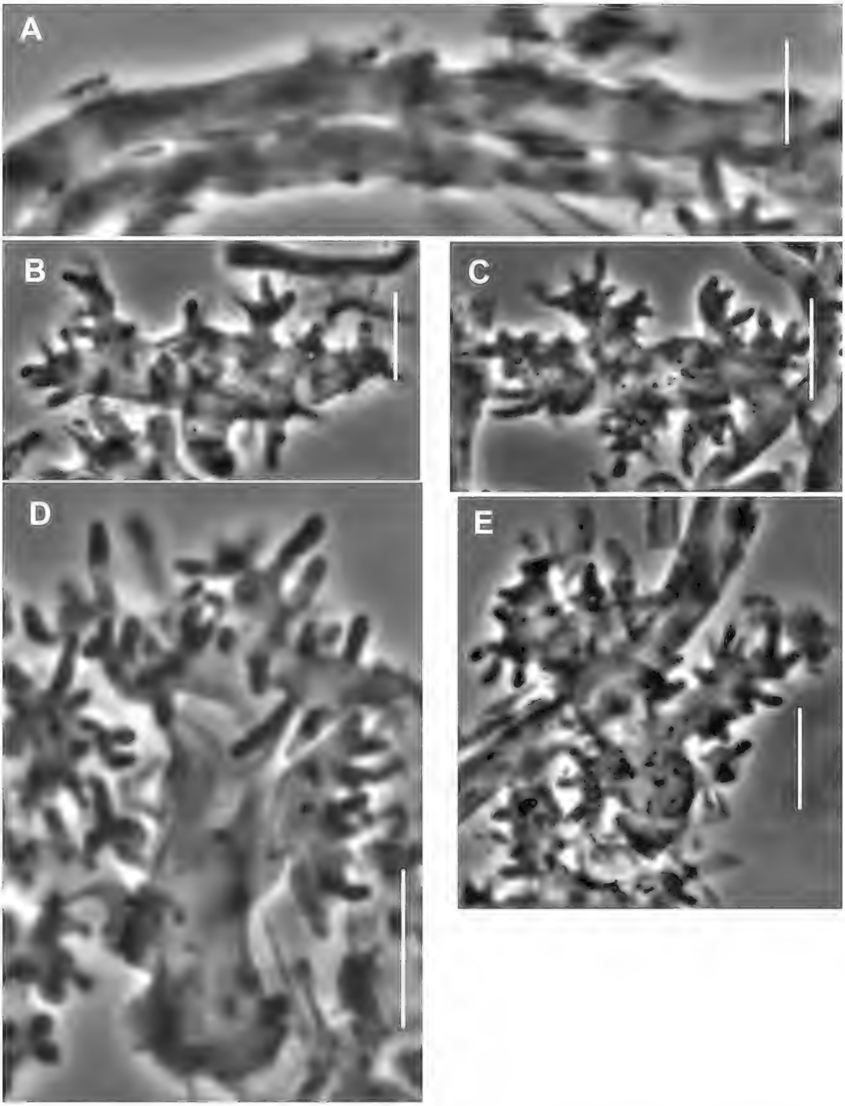

Fig. 52. *Pseudomarasmius quercophiloides* (TENN-F-049179, holotype). Pileipellis elements. A. Repent, encrusted hypha. B,C. Diverticulate hyphae. D,E. Broom cell-like hyphal termini. Scale bars: 10 µm.

diverticula digitate (not conical), 1–8 × 0.7–1.1 µm, often slightly gnarled, dense (PhC); and 3) diverticulate broom cell-like hyphal termini (Fig. 52d,e),

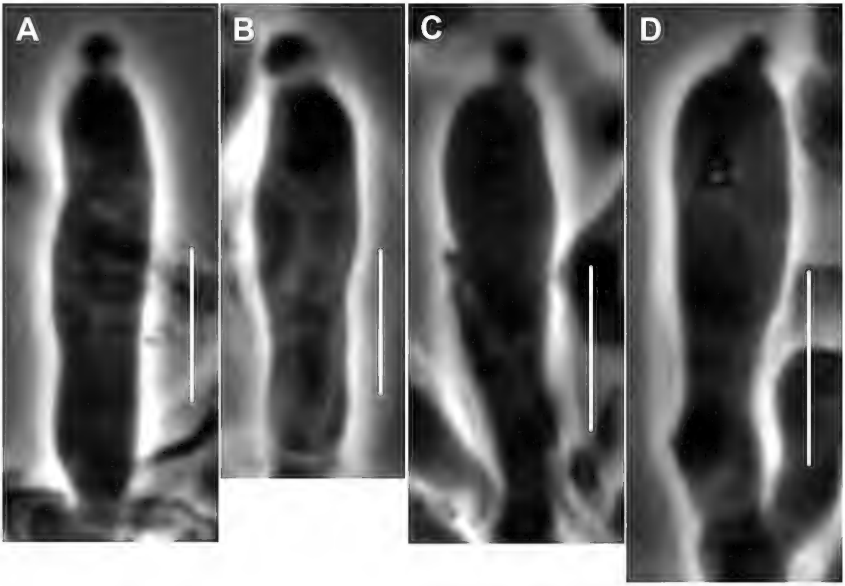

Fig. 53. *Pseudomarasmius quercophiloides* (TENN-F-049179, holotype). Pleurocystidia. Scale bars: 10 µm.

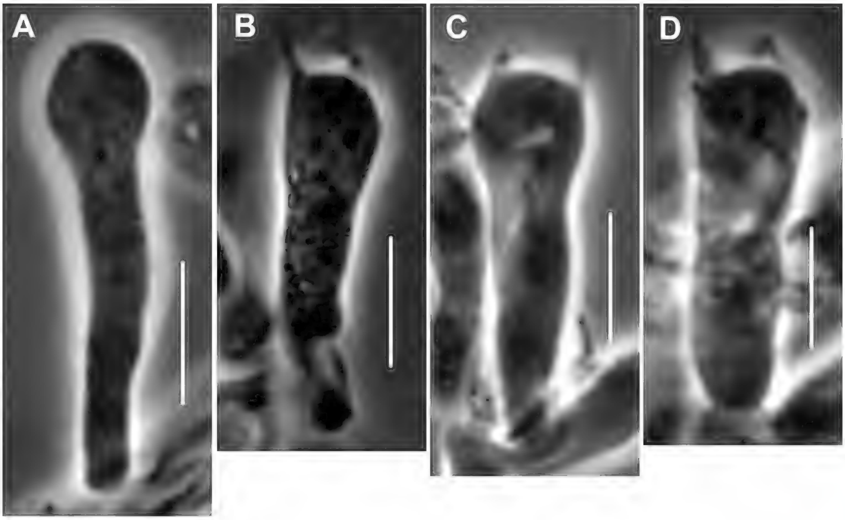

Fig. 54. *Pseudomarasmius quercophiloides* (TENN-F-049179, holotype). A. Basidiole. B–D. Basidia. Scale bars: 10 µm.

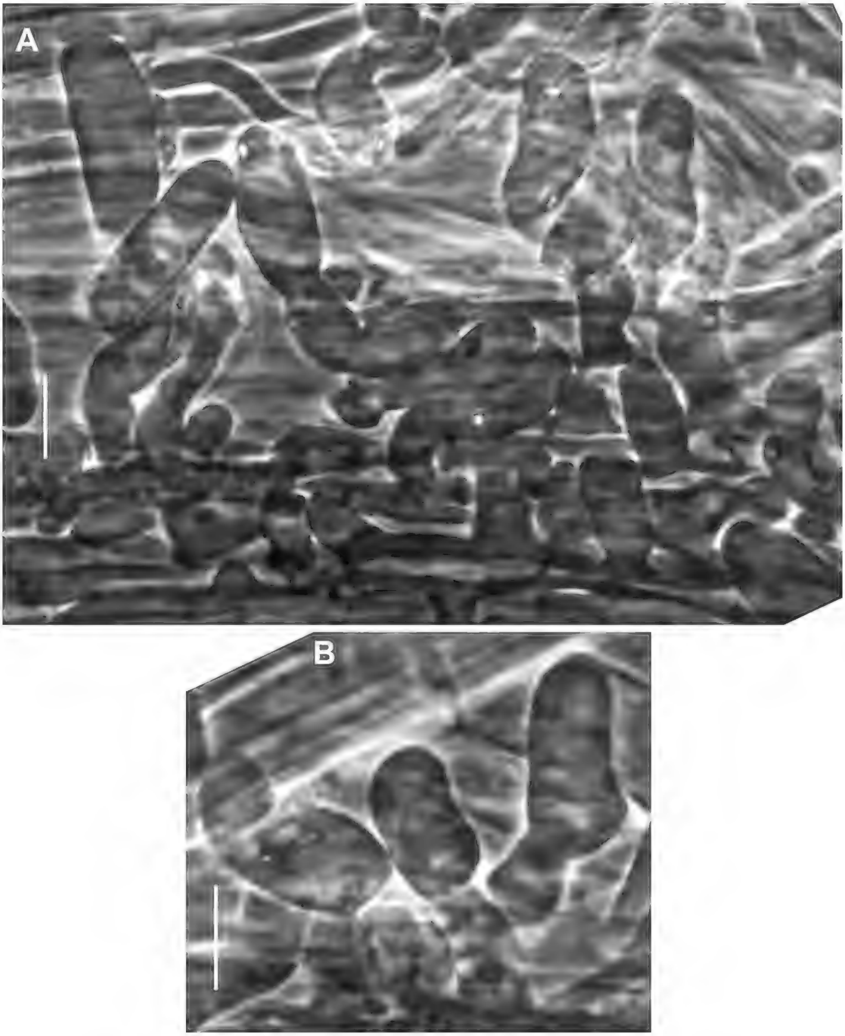

FIG. 55. *Pseudomarasmius quercophiloides* (TENN-F-049179, holotype). Clusters of upper stipe caulocystidia. Scale bars: 10 µm.

similar to diverticulate hyphae, without clamp connections. No evidence of gelatinization observed in pileipellis. Pileus trama loosely interwoven; hyphae 2–5.5 um diam, thin-walled, hyaline, without clamp connections. Hymenium composed of three elements with no evidence of gelatinization: 1) PLEUROCYSTIDIA (FIG. 53) occasional (not abundant), 19–24 × 5–6 um, fusiform to narrow-fusiform, often with small, subglobose, apical

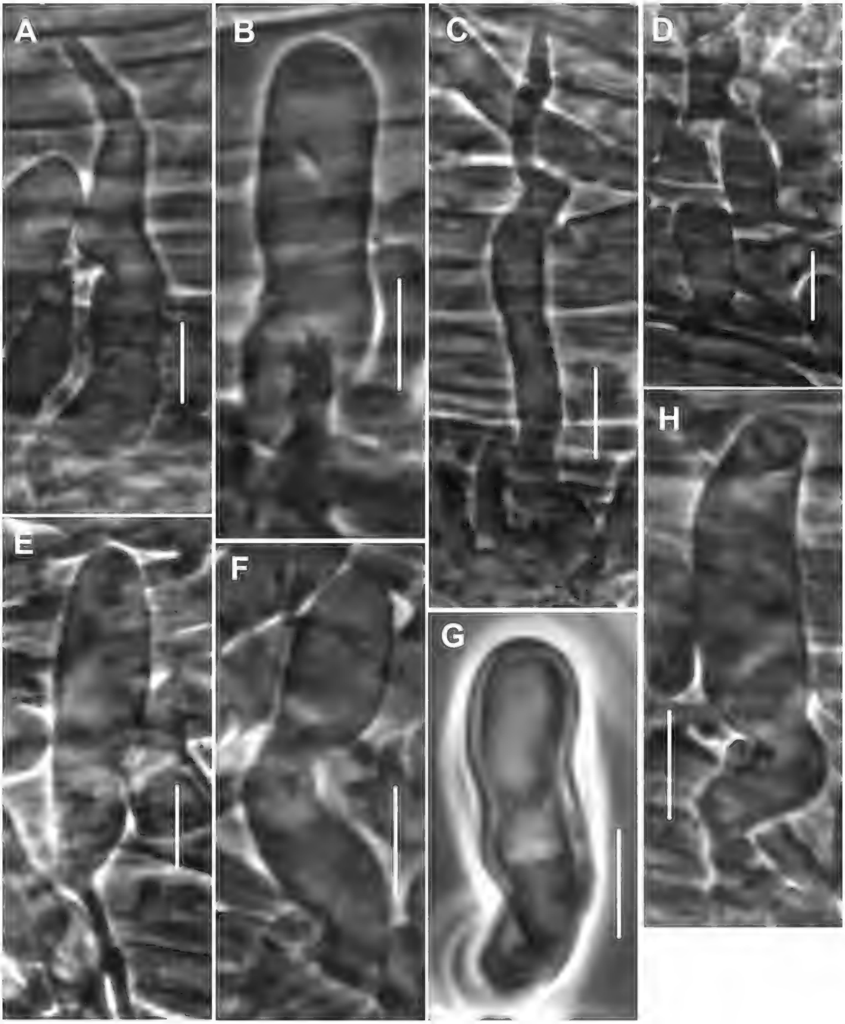

Fig. 56. *Pseudomarasmius quercophiloides* (TENN-F-049179, holotype). Individual upper stipe caulocystidia. Note caulocystidial origins in D. Scale bars: 10 µm.

protuberance (appearing mammilate), without clamp connections; 2) basidioles (Fig. 54a) clavate to subcapitulate, without clamp connections; basidia (Fig. 54b–d) (22–)27–30 × 6–7 µm, 4-sterigmate (sterigmata slender, easily collapsed), without clamp connections; and 3) cheilocystidia not observed. Basidiospores (Fig. 49c) 6–7 × 3–4(–5) µm (Q = 1.40–1.86;

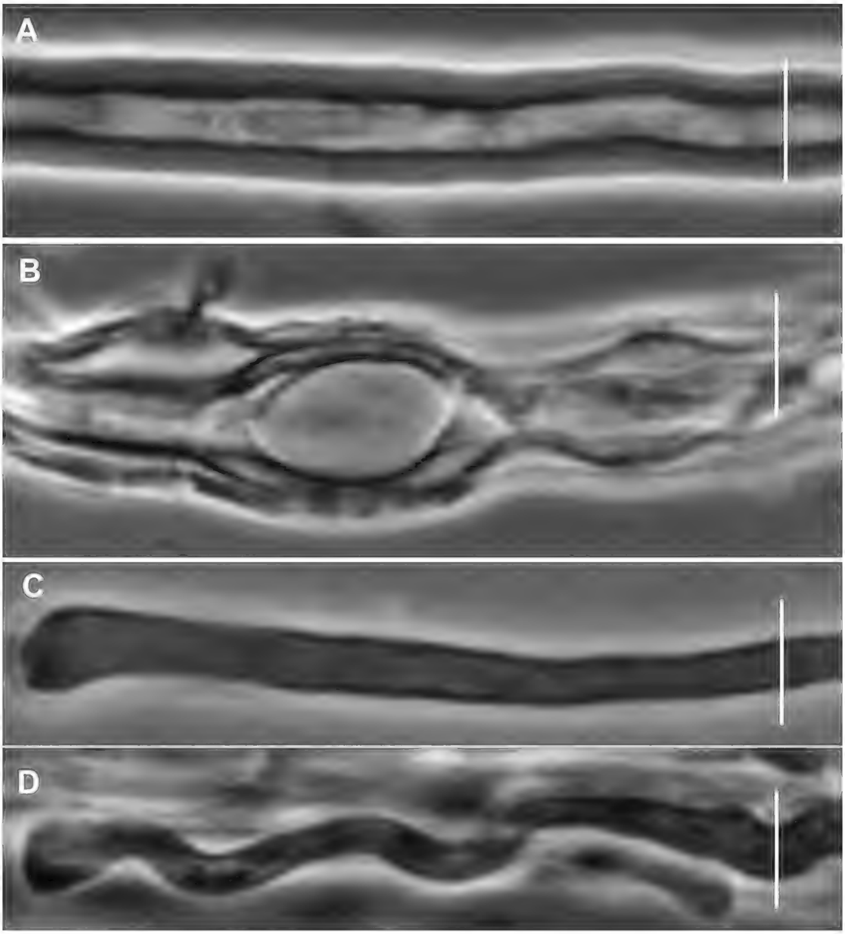

Fig. 57. *Pseudomarasmius quercophiloides* (TENN-F-049179, holotype). Lower stipe medullary hyphae. A. Stout, thick-walled hypha. B. Gelatinized or shredded stout hypha. C. Slender hypha. D. Serpentine slender hypha. Scale bars: 10 µm.

E^m = 1.53; L^m = 6.60 µm), ellipsoid, not tapering proximally, thin-walled, hyaline, inamyloid. Upper stipe medullary hyphae <12 µm diam, strictly parallel, free (no evidence of gelatinization), hyaline, with no clamp connections, thick-walled (wall ≤1.5 µm thick). Upper stipe cortical hyphae 4–6 µm diam, thick-walled (wall ≤1 um thick), strongly pigmented (olive brown, PhC), without clamp connections, decorated with numerous caulocystidia (Fig. 55); caulocystidia (Fig. 56) 3–30(–40) × 7–13 um,

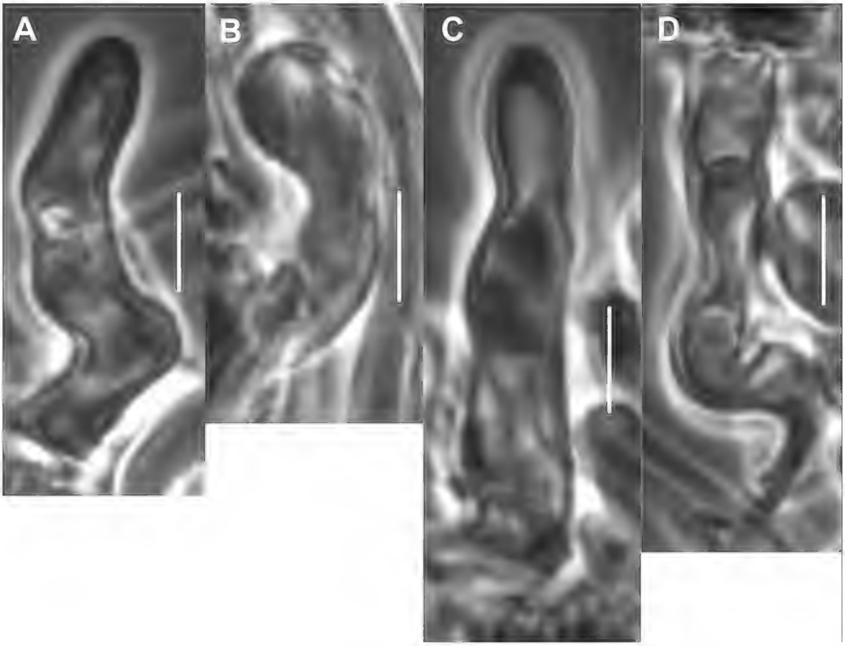

FIG. 58. *Pseudomarasmius quercophiloides* (TENN-F-049179, holotype). Individual lower stipe caulocystidia. Scale bars: 10 µm.

lobate to thumb-shaped, usually gnarled or constricted, firm- to thick-walled (wall ≤1 µm thick), weakly pigmented, arising as constricted side branches of surface cortical hyphae. Lower stipe medullary hyphae strictly parallel, of two types: 1) 5–8 µm diam, thick-walled (wall ≤2 µm thick), occasionally gelatinized (FIG. 57A) or shredded (FIG. 57B); and 2) slender, 2–2.5 um diam, thin-walled, straight (FIG. 57C) to serpentine (FIG. 57D), with dense contents (PhC). Lower stipe cortical hyphae 3.5–6 µm diam, thick-walled (wall ≤2 µm thick, often obscuring cell lumen), densely pigmented (dark olive brown, PhC), beset with crowded caulocystidia; CAULOCYSTIDIA (FIG. 58) 5–30 × 8–13 um, crowded, stout-vermiform, usually gnarled and/or constricted, thin- to thick-walled (wall ≤1 µm thick), hyaline to weakly pigmented proximally. Resupinate rhizomorph anatomy similar to that of lower stipe. Cortical hyphae with superficial film of gelatinous material (FIG 59A) acting as adhesive to the leaf surface. Rhizocystidia (FIG. 59B–E) widely scattered, similar to caulocystidia but thick-walled (wall ≤1.5 µm thick) and strongly pigmented.

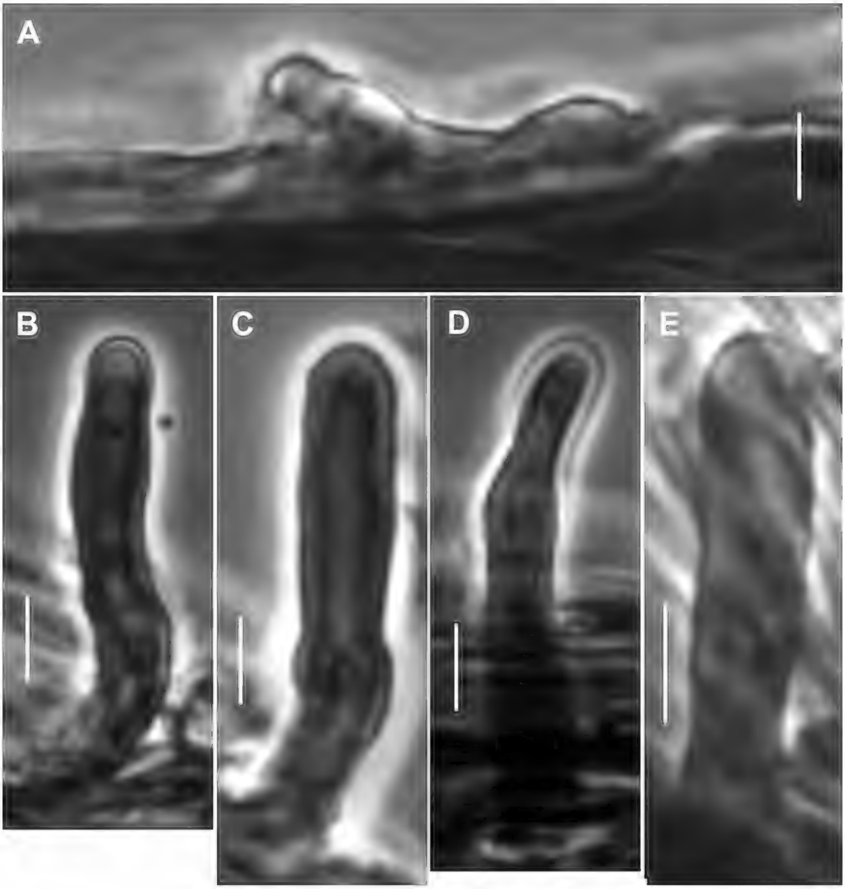

Fig. 59. *Pseudomarasmius quercophiloides* (TENN-F-049179, holotype). Rhizomorph anatomy. A. Surface of cortex with suggestion of superficial gel. B–E. Rhizocystidia. Scale bars: 10 µm.

Commentary: Similarities with *G. quercophilus*: 1) abundant rhizomorphs, not black (in *G. quercophilus* chestnut brown to red-brown), dominantly resupinate on sclerophyllous hardwood leaves; 2) pleurocystidial general shape and size; 3) pileus sulcate-striate with small umbo; and 4) basidiomata arising from leaf surface not from rhizomorphs. Dissimilarities to *G. quercophilus* include: 1) clamp connections lacking; 2) absence of cheilocystidia; 3) presence of pruinose caulocystidia.

The ITS sequence of *Ps. quercophiloides* is largely identical to GenBank sequence KF251072, deposited as *Gymnopus glabrocystidiatus* (not holotype) from South Korea (2 bp difference in 636bp). Geographical proximity and sequence homology suggest that these likely represent the same taxon.

Additional specimen examined: **CHINA, Yunnan Prov., Jinhong Pref.**, vic. Menghai, Xishuangbanna Nature Reserve, 8.VIII.990, coll. RHP, Q Wu, Li, TFB 3148 (TENN-F-049179)

Pseudomarasmius straminipes (Peck) R.H. Petersen, **comb. nov.** Figs 60–64

IF 555734

≡ *Marasmius straminipes* Peck, Bull. Buffalo Soc. Nat. Sci. 1: 59.

≡ *Chamaeceras straminipes* (Peck) Kuntze, Revis. Gen. P. 3(2): 457.

Holotype (implicit, Peck): United States, New York, Albany Co, Center (= Kamer), 42°39′10″N 73°45′52″W, Oct. 1872. C.H. Peck (NYS!).

Diagnostic characters include: 1) stipe capillary, buff above, ochraceous downward, glabrous-shining; 2) rhizomorphs usually common, pallid; 3) fruiting on fallen conifer needles, usually spruce/fir; 6) distribution in eastern North America.

Basidiomata (Fig. 60a) diminutive, marcescent, reviving. Pileus (1.5–) 3–7 mm broad, hemispherical or convex, expanding to plano-convex, occasionally with suggestion of low umbo, dull, opaque, glabrous or minutely suede-like, light brown (7D4-5) or pale greyish brown (7D3) overall when young, soon fading to pale brownish orange (7C3) or pale brownish grey (6B2, 6C3); disc smooth or weakly rugulose; margin rugulose-striate or rugulose but not striate, soon fading to greyish orange (6C2) or pale greyish orange (5B2), in age with a hint of grey and buff; context thin, buff, often fading to whitish, buff or pinkish buff overall. Lamellae adnate, subdistant, without anastomoses or interveining, narrow, whitish or buff when young, becoming greyish buff or pale brownish grey (6C3) in age; edges even or crystalline-fimbriate; lamellulae in 1–2 series. Stipe 10–35 × 0.2–0.5 mm, terete, equal, tough, rigid or wiry, glabrous-shining, sometimes tacky, hollow, instititious, brownish orange (5C4, especially downward) to yellow (4A5-6) or straw-colored overall when young or with a slightly paler apex, darkening overall with age to stramineous, becoming slightly more brownish at maturity, never dark brown or black. Rhizomorphs (Fig. 60A) extensive, with short resupinate lengths on needle surface, then loosely curly, <20 × 0.1–0.3 mm, repeatedly branched with branches often long and flagelliform, glabrous, dull yellow-brown in basal parts, champagne colored upward and finally off-white. Odor and taste negligible.

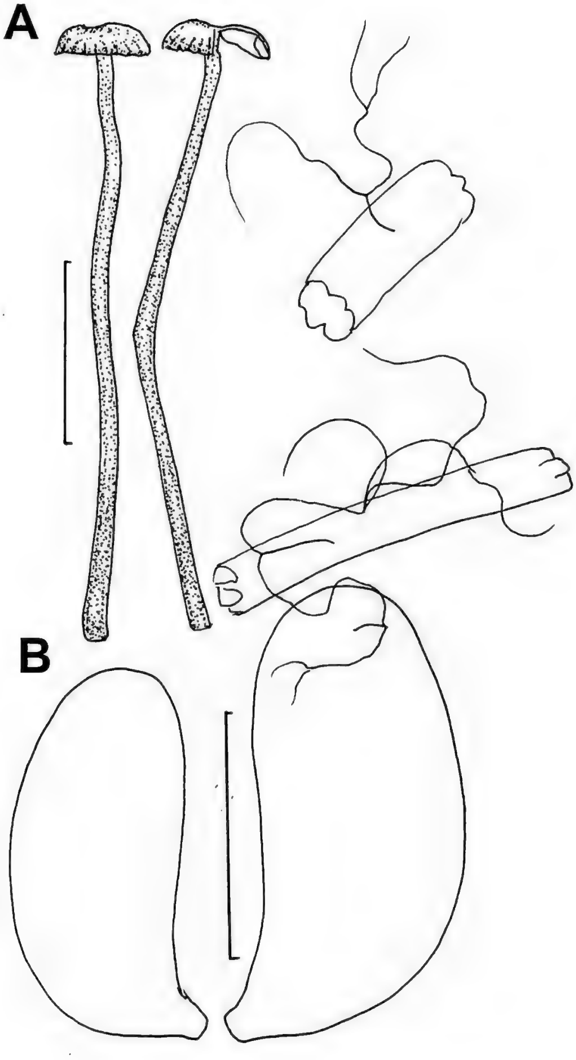

Fig. 60. *Pseudomarasmius straminipes* (TENN-F-026266).
A. Basidiomata and rhizomorphs. B. Basidiospores. Scale bars: A = 10 mm; B = 5 µm.

Habitat & phenology: Gregarious to scattered to dead conifer needles including *Picea/Abies* and *Pinus* (especially *P. strobus*); eastern North America [reported by Desjardin & Petersen (1989a) from Alabama, New Jersey, New York, North Carolina, Ohio and Tennessee]; summer–autumn.

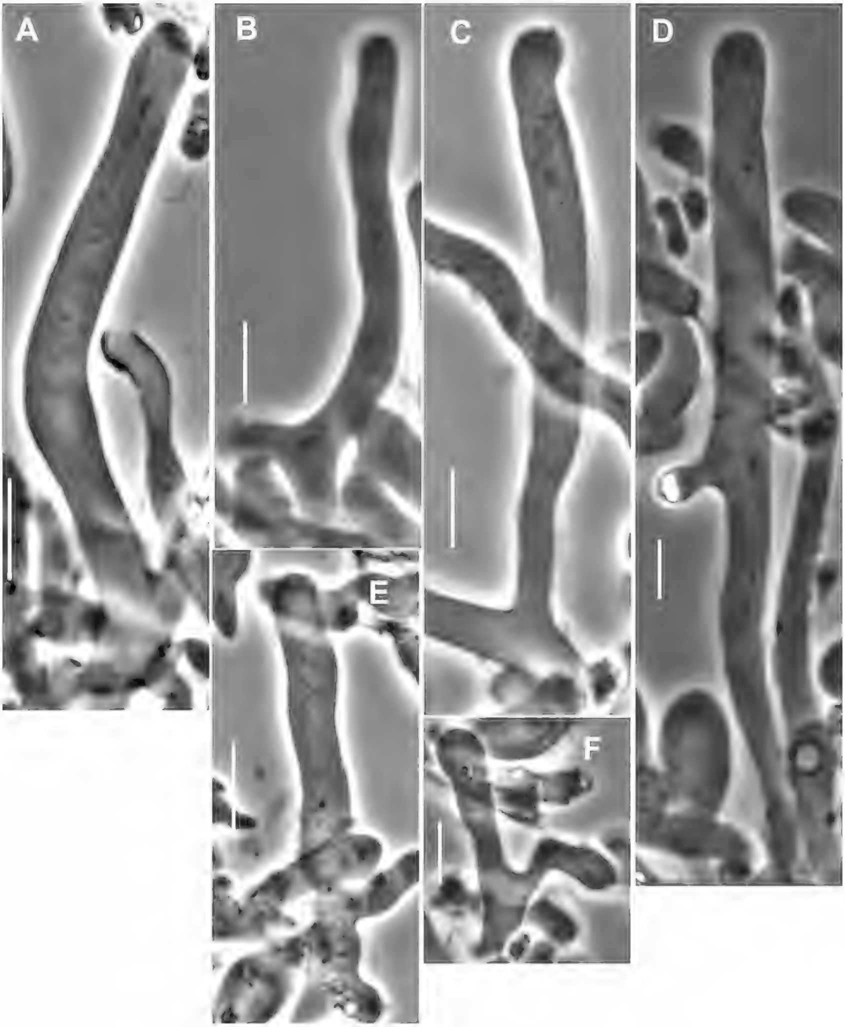

Fig. 61. *Pseudomarasmius straminipes* (TENN-F-047638).
Pileipellis hairs. Note production of abortive side branch. Scale bars: 10 µm.

Pileipellis without evidence of slime matrix, a well-developed *Rameales*-structure, of the following elements: 1) pileal hairs (Fig. 61) densely scattered, ≤80 × 4–6 µm, firm-walled, cylindrical, without clamp connections, often with aborted side branch, hyaline, usually subcapitulate; 2) repent hyphae 4–8.5(–15) µm diam, thin- to firm-walled, without clamp

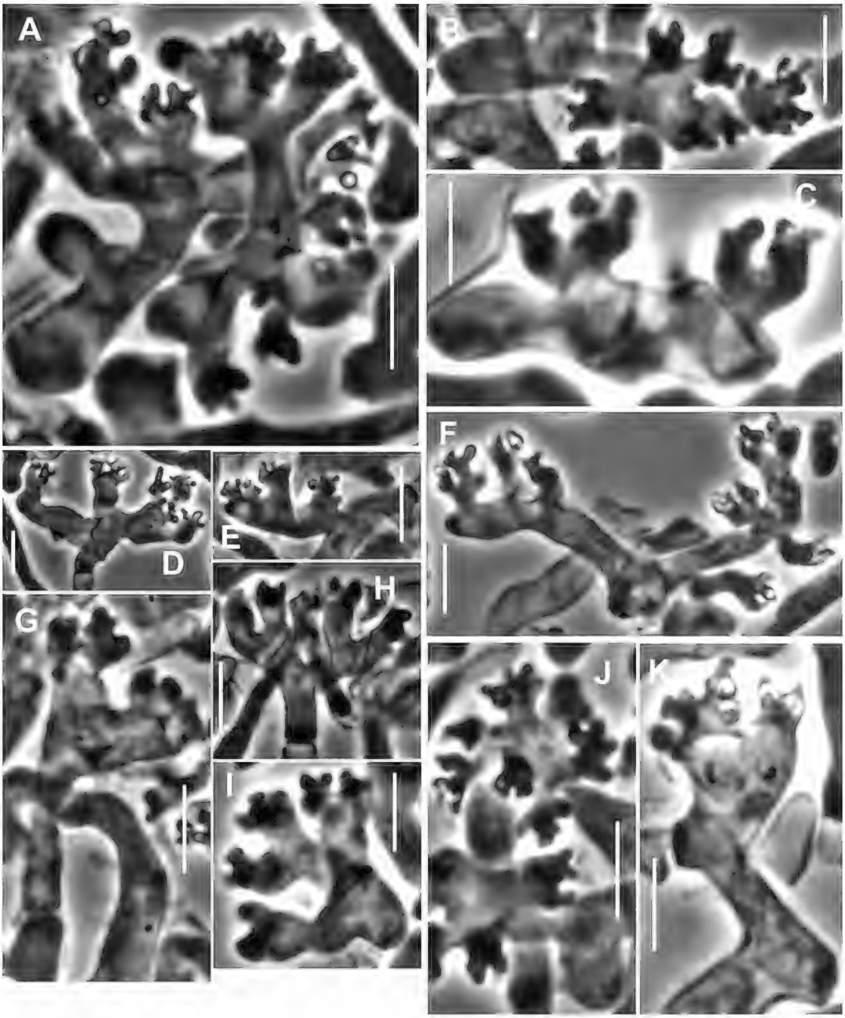

Fig. 62. *Pseudomarasmius straminipes* (TENN-F-047642). Pileipellis elements. A–C. Diverticulate hyphae. D–K. Broom cell-like hyphal termini. Scale bars: 10 µm.

connections, strongly to weakly encrusted (crust material in scabs with vaguely annular to spiral patterning but occasionally protruding and then resembling diverticula); 2) scattered repent diverticulate hyphae (Fig. 62a–c) irregular in outline, often lobed, 2.5–8(–12) µm diam, hyaline to pale brownish, smooth or weakly encrusted, inamyloid; diverticula 1–8 × 1–3

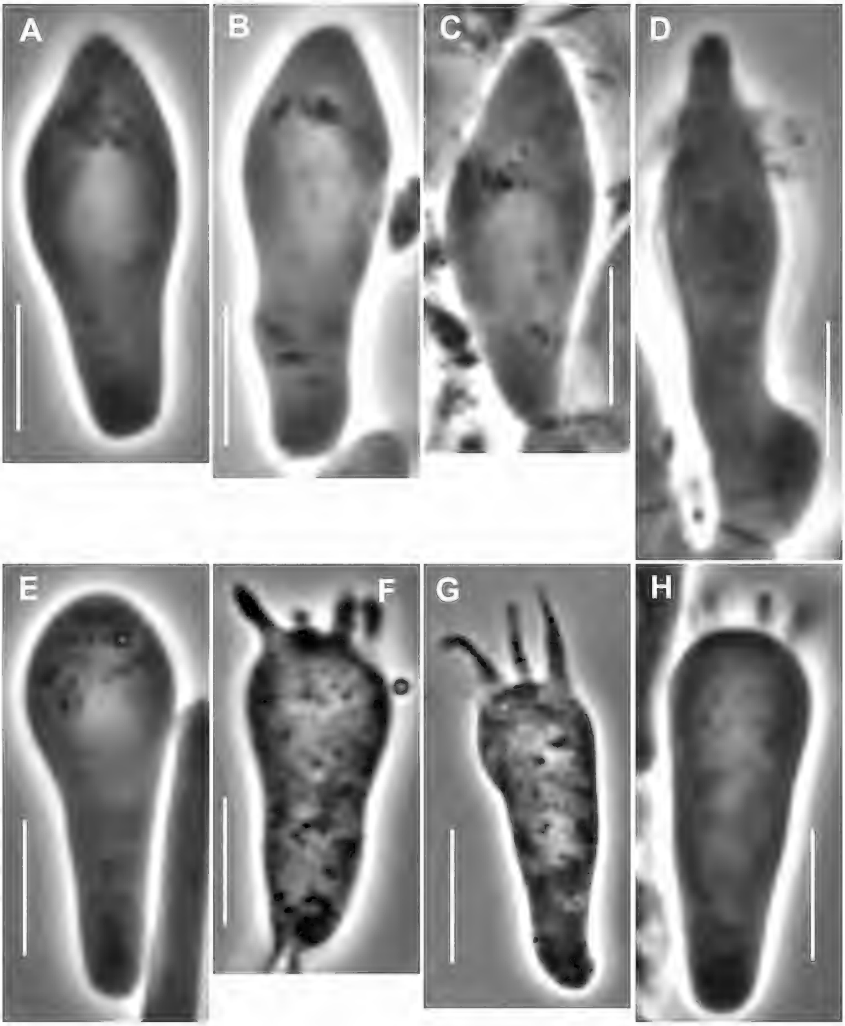

Fig. 63. *Pseudomarasmius straminipes* (TENN-F-047638). Hymenial structures. A–D. Pleurocystidia. E. Basidiole. F–H. Basidia. Scale bars: 10 µm.

µm, knob-like, often dichotomous and in fascicles, obtuse, thin-walled; and 3) broom cell-like hyphal termini (Fig. 62d–k) common, stalked (stalk 4–8 × 3.5–5.5 µm, without clamp connections), usually branched, distally variously lobed to diverticulate; diverticula 1–5 × 1–1.5 µm, nodulose, subrefringent, often appearing dichotomous. Pileus trama interwoven; hyphae 28–11)

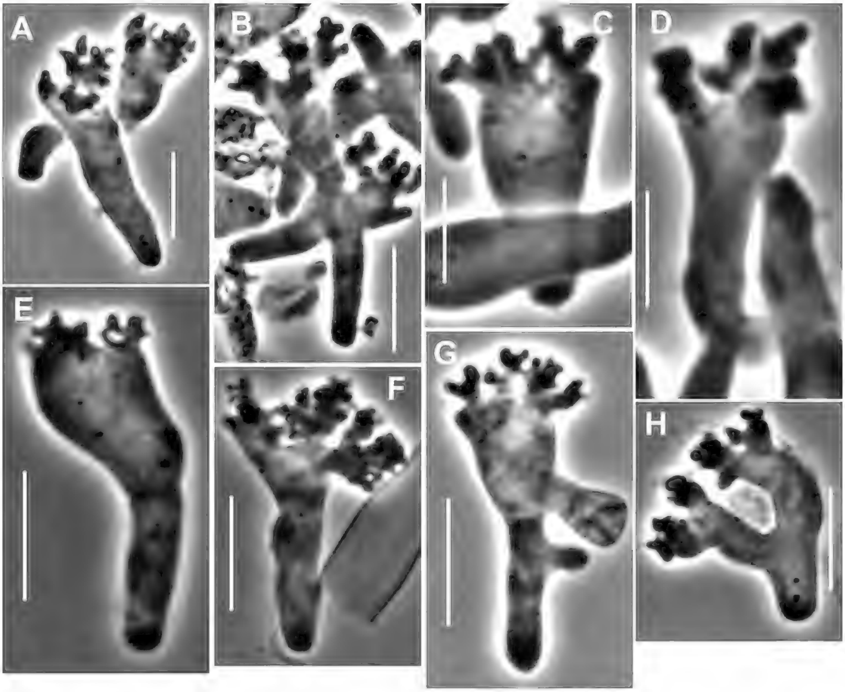

FIG. 64. *Pseudomarasmius straminipes* (TENN-F-047638).
Cheilocystidia. Note suggestion of dichotomous setulae. Scale bars: μm.

μm diam, inflated or not, hyaline, inamyloid, thin-walled, smooth or weakly incrusted; incrustations granular or often helical and yellowish to pale brownish. Lamellar tramal hyphae similar to pileus tramal hyphae, but hyaline and non-encrusted throughout, without clamp connections. PLEUROCYSTIDIA (FIG. 63A–D) abundant, 21–26(–29) × 5–8 μm, fusiform to fusiform-rostrate, without clamp connections; contents more or less homogeneous. Basidioles (FIG. 63E) clavate; BASIDIA (FIG. 63F–H) 19–28 × 6.4–10 μm, clavate, (2–)4-sterigmate, without clamp connections; contents more or less homogeneous; effete basidia emptying but not collapsing ("husking"). BASIDIOSPORES (FIG. 60B) 6.5–9.5 × 3.2–4.5 μm ($Q = 1.70–2.40$; $E^m = 2.00$; $L^m = 8.00$ μm), ellipsoid, slightly tapered proximally, smooth, hyaline, inamyloid; spore deposit whitish. CHEILOCYSTIDIA (FIG. 64) scattered to abundant, 13–23(–33) × 10–15 μm 4.5–8(–11) μm, stalked (stalk ≤2–6 × 3.5–8 μm, thin-walled, without clamp connections), unbranched or once-branched (and then branches short, stout), often lobed, setulose, hyaline, firm-walled; setulae 1–4 × 0.5–2 µm, sub-refringent, often saddle-shaped to dichotomous). Stipe medullary hyphae 3.5–7(–10) µm diam, strictly parallel, firm- to thick-walled (wall ≤0.5 µm thick, hyaline, Melzer's reagent) without evidence of slime matrix (Melzer's reagent, PhC), without clamp connections. inamyloid. Stipe cortical hyphae 1.5–6.5 µm diam, strictly parallel, thick-walled (walls ≤2.5 µm thick, non-encrusted), smooth, yellowish or pale brownish orange, moderately dextrinoid (Melzer's reagent + BF). Rhizomorph tissue similar to that of the stipe, with dextrinoid cortical hyphae. Clamp connections absent on all tissues.

Commentary: Protologue (Peck 1873 Bull. Buffalo Soc. Nat. Sci. 1(2): 59.): "Pileus membranaceous, hemispherical or convex, smooth, striate, whitish; lamellae distant, unequal, white; stem corneous, smooth, shining, filiform, inserted, pale straw colored. Plant 1″–2″ [inches] high, pileus 1″–3″ [lines] broad. Fallen leaves of pitch pine, *Pinus rigida*. Center [N.Y.] October."

After examination of the type specimen of *M. straminipes*, Gilliam (1976: 136) opined that: "The type specimen is closest to *Marasmiellus*," and reviewed some putative diagnostic characters. In the same publication, Gilliam (1976: 131) reported on another Peck taxon, *M. filopes* Peck, basidiomata of which are similar to those of *M. straminipes*, and stated: "There is too little left of the specimen to section," but concluded that "*M. filopes* is nearest *Marasmiellus*." Transfers of neither species (*M. straminipes*, *M. filopes*) to *Marasmiellus*, however, were formally accomplished. Redhead (1980), in his treatment of *Marasmiellus filopes*, did not mention or compare *M. straminipes* (validly published by Peck 1873, repeated in 1874), but, like Gilliam (1976), considered *M. filopes*, *M. thujinus* Peck, and *M. piceina* Kauffman as taxonomic synonyms. In a later discussion of clampless *Marasmius* taxa, Redhead (1984) rejected Gilliam's (1976) opinion of *M. straminipes* as *Marasmiellus*, retaining the species in *Marasmius* sect. *Androsacei*, but without mention of *Marasmiellus filopes* and its synonyms. Redhead (1984) mentioned the clampless state of *M. straminipes* by way of comparison with *M. pallidocephalus*. Desjardin (1989) examined Peck's type specimens of *M. straminipes* and *M. filopes*. Still later, in a paper redescribing *Marasmius straminipes* (Desjardin & Petersen 1989b), *M. straminipes* was again reported as clampless and Redhead's (1984) retention of *M. straminipes* in *Marasmius* sect. *Androsacei* was accepted, but *M. filopes* was not mentioned. In addition to the characters dictating placement of *M. straminipes* in *Marasmius* for Redhead (1984), Desjardin & Petersen

(1989b) added the dextrinoid reaction on stipe medullary hyphae in *M. straminipes*, theretofore unknown in *Marasmiellus*.

Description of basidiomata exhibiting clamp connections and those lacking clamps as forms or varieties of the same species is commonly found in the literature. Often, the clampless state is found accompanied by 2-sterigmate basidia and somewhat larger basidiospores than expected (see such forms in *Hymenopellis*, Petersen & Hughes 2010; and in *Mycena*, Kühner 1938, Lamoure 1957a,b, 1959, 1960). Upon further study, such forms may be found to be technically anamorphic (asexual) structures reproducing without meiosis and existing in a haploid state. In clampless forms in *Gymnopus* subg. *Gymnopus*, however, basidia appear to be 4-sterigmate and basidiospore metrics conform to the norms expected. Causes for such correlation remain opaque. In background research resulting in this paper, *Ps. efibulatus* was first noted as a clampless form of an undescribed *Marasmius* species. *Marasmius straminipes* (clampless) was thought to have a variety with clamp connections (*M. straminipes* var. *fibulatus* Desjardin & R.H. Petersen 1989. Bull. Torrey Bot. Club 49: 184.) With the proposal of *Pseudomarasmius*, a different avenue is offered, with molecular analyses important. DNA sequences of the analogous forms might clarify taxonomy, but so far such sequences have not been produced.

The proposed transfer of *M. straminipes* to *Pseudomarasmius* is based on morphological characters: unfortunately, sequences derived from *M. straminipes* basidiomata have consistently been "dirty," with more than one simultaneous sequence overlapping one another. The close resemblance to *Ps. glabrocystidiatus* in form, ecology, and microstructure, however, makes our transfer relatively comfortable.

Specimens examined: **UNITED STATES, North Carolina, Macon Co.**, vic. Otto, Coweeta Hydrologic Laboratory, Ball Creek area, 35°02′58″N 83°26′20″W, 13.VIII.1987, coll. D.E. Desjardin, DED 4458 (TENN 47642); vic. Highlands, Blue Valley, ca 3 mi up Clear Creek Rd., 9.VII.1991, coll. D.E. Desjardin, DED 5149 (TENN-F-050018, SFSU); **Swain Co.**, vic. Bryson City, GSMNP, Clingman's Dome, 1.VIII.1989, coll. S.A. Gordon, TFB 2125 (TENN-F-049143). **Tennessee, Sevier Co.**, GSMNP, Old Indian Gap Road off Clingman's Dome Road, 11.VI.1986, coll. D.E. Desjardin, DED 3578 (TENN-F-047638); Indian Gap, 35°36′34″N,83°26′47″W, 12.VI.1952, coll. L.R. Hesler (as *Marasmius* sp.), det. D.E. Desjardin (TENN-F-026266).

General discussion

The clampless state has always raised questions about nuclear behavior in the basidial primordium and basidiospores (see Petersen 1995). Often, the clampless state is accompanied by 2-sterigmate basidia, with the ploidy of parent mycelium, dikaryotization, meiosis and subsequent mitosis unclear (Petersen 1978). In *Pseudomarasmius,* however, the clampless state seems coupled with 4-sterigmate basidia (rarely 2-sterigmate in *Ps. pallidocephalus* and *Ps. nidus-avis*). This allows some conjecture that parent mycelium was dikaryotic, with diploidization in the basidial primordium probable, although nuclear segregation in the basidium and nuclear number in the basidiospores remains unknown. Clarifying experiments in this situation cannot be assumed by culturing single basidiospores and pairing resultant cultures, for the nuclear condition of the "monokaryons" is unknown until observed Cytogenetic evidence must be gathered directly, usually with the aid of DAPI staining and phase contrast microscopy or some more cumbersome stains (Restivo & Petersen 1976, Hubbard & Petersen 1979).

In an entirely different direction, if any doubt remains, morphological identification and especially generic (or infrageneric) placement has become almost impossible in large groups of marasmioid fungi. *Gymnopus* in the sense of Wilson & Desjardin (2005), especially, has been repeatedly shown to form a monophyletic clade but inclusive of disparate basidiomatal morphology, ranging from *G. androsaceus* (traditionally type of *Marasmius* sect. *Androsacei*) and *G. perforans* (traditionally type of *Micromphale* sect. *Perforantia*) rather typical of marasmioid stature, to *G. fusipes* (typus generis) forming much larger, coarser and fasciculate basidiomata, and *Caripia* which forms only a subclavarioid hymenophore. Typical *Micromphale* (*M. venosum* typus generis), with gelatinized tissue layer in the pileus trama, also is now found in the *Gymnopus* clade (see Fig. 1).

In another different taxonomic direction, *Mycetinis* (and *Paramycetinis*, see above), *Rhodocollybia, Lentinula, Connopus*, and *Pseudomarasmius* (see above), all traditionally within larger genera, are now known to resolve as monophyletic clades (see Fig. 1).

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Bibliography

Aldrovandi MSP, Johnson JE, O'Meara BC, Petersen RH, Hughes KW. 2015. The *Xeromphalina campanella/kauffmanii* complex: species delineation and biogeographical patterns of speciation. Mycologia 107: 1270–1284. https://doi.org/10.3852/15-087

Antonín V, Halling RE, Noordeloos ME. 1997. Generic concepts within the groups of *Marasmius* and *Collybia* sensu Lato. Mycotaxon 63: 359–368.

Antonín V, Noordeloos ME. 2010. A monograph of marasmioid and collybioid fungi in Europe. IHV-Verlag, Eching.

Antonín V, Ryoo R, Ka K-H. 2014. Marasmioid and gymnopoid fungi of the Republic of Korea. 7. *Gymnopus* sect. *Androsacei*. Mycological Progress 13: 703–718. https://doi.org/10.1007/s11557-013-0953-z

César E, Bandala VM, Montoya L, Ramos A. 2018. A new *Gymnopus* species with rhizomorphs and its record as nesting material by birds (*Tyrannideae*) in the subtropical cloud forest from eastern Mexico. MycoKeys 42: 21–34. https://doi.org/10.3897/mycokeys.42.28894

Cleland JB. 1934. Toadstools and mushrooms and other larger fungi of South Australia (addenda) Pt. 1. Government Printer, Adelaide.

Cooper JA, Leonard PL. 2013 Three new species of foetid *Gymnopus* from New Zealand. MycoKeys 7: 31–44. https://doi.org/10.3897/mycokeys.7.4710

Dentinger BTM, Gaya E, O'Brien H, Suz LM, Lachlan R, Díaz-Valderrama JR, Koch RA, Aime MC. 2016. Tales from the crypt: genome mining from fungarium specimens improves resolution of the mushroom tree of life. Biological Journal of the Linnean Society 117: 11–32. https://doi.org/10.1111/bij.12553

Desjardin DE. 1989. The genus *Marasmius* from the southern Appalachian Mountains. Knoxville, Tennessee: University of Tennessee.

Desjardin DE. 1990. Culture morphology of *Marasmius* species. Sydowia 42: 17–87.

Desjardin DE, Horak E. 1997. *Marasmius* and *Gloiocephala* in the South Pacific region: Papua New Guinea, New Caledonia, and New Zealand taxa. Bibliotheca Mycologica 168: 1–152.

Desjardin DE, Petersen RH. 1989a. Studies on *Marasmius* from eastern North America. I. *Marasmius straminipes* and a new variety. Memoirs of the New York Botanical Garden 49: 181–186.

Desjardin DE, Petersen RH. 1989b. Studies on *Marasmius* from eastern North America. III. *Marasmius brevipes* and *Micromphale* sect. *Rhizomorphigena*. Mycologia 81: 76–84. https://doi.org/10.1080/00275514.1989.12025628

Desjardin DE, Retnowati A, Horak E. 2000. Agarics of Indonesia. 2. A preliminary monograph of *Marasmius* from Java and Bali. Sydowia 52: 92–193.

Earle FS. 1909. The genera of the North American gill fungi. Bulletin of North York Botanical Garden 5: 373–462.

Eygelsheim WFT. 1981 Tasmanian mushrooms and toadstools. Burnie Adult Education Publishing Group, Burnie, Australia.

Farnet AM, Roux M, LePetit J. 1999. Genotypic variations among isolates of *Marasmius quercophilus*. A white-rot fungus isolated from evergreen oak litter. Canadian Journal of Botany 77: 884–890. https://doi.org/10.1139/b99-051

Fries E. 1821. Systema mycologicum. Lundae 1. 520 p.

Fuhrer B. 1985. A field companion to Australian fungi. Five Mile Press.

Fuhrer B, Robinson R. 1972. Rainforest fungi of Tasmania and south-east Australia. CSIRO, East Melbourne, Australia.

Geneious. 2017. Geneious version 11.0.3 http://www.geneious.com/

Gilliam MS. 1975. New North American species of *Marasmius*. Mycologia 67: 817–844. https://doi.org/10.1080/00275514.1975.12019811

Gilliam MS. 1976. The genus *Marasmius* in the northeastern United States and adjacent Canada. Mycotaxon 4: 1–44

Grgurinovic CA. 1997. Larger fungi of South Australia. Botanical Garden Adelaide & State Herbarium.

Hagiwara Y, Matsuoka S, Hobara S, Mori AS, Hirose D, Osono T. 2015. Bleaching of leaf litter and associated microfungi in subboreal and subalpine forests. Canadian Journal of Microbiology 61: 735–743. https://doi.org/10.1139/cjm-2015-0111

Halling RE. 1983. The genus *Collybia* (*Agaricales*) in the northeastern United States and adjacent Canada. Mycologia Memoirs 8. 148 p.

Hintikka V. 1970. Studies on white-rot humus formed by higher fungi in forest soils. Communicationes Instituti Forestalis Fenniae 69: 1–68.

Horak E. 1971a. A contribution toward the revision of the *Agaricales* (*Fungi*) from New Zealand. New Zealand Journal of Botany 9: 403–462. https://doi.org/10.1080/0028825X.1971.10430193

Horak E. 1971b. Contributions to the knowledge of the *Agaricales* s.l. (*Fungi*) of New Zealand. New Zealand Journal of Botany 9: 463–493. https://doi.org/10.1080/0028825X.1971.10430194

Hubbard M, Petersen RH. 1979. Studies in basidial nuclear behavior of selected species of clavarioid and cantharelloid fungi. Beihefte zur Sydowia 8: 209–223.

Hughes KW, Petersen RH, Johnson JE, Moncalvo J-M, Vilgalys R, Redhead SA, Thomas T, McGhee L. 2001. Infrageneric phylogeny of *Collybia* ss. str. based on sequences of ribosomal ITS and LSU regions. Mycological Research 105: 164–172. https://doi.org/10.1017/S0953756200003415

Korf RP. 1973. Chapter 9. *Discomycetes* and *Tuberales*. 249–319, in: GC Ainsworth & al. (eds). The Fungi, an Advanced Treatise, Volume IVA A Taxonomic Review with Keys: Ascomycetes and Fungi Imperfecti. Academic Press, New York.

Kornerup A, Wanscher JH. 1967. Methuen handbook of color. 2nd revised edition Methuen Co, London. 243 p.

Kühner R. 1938. Le genre *Mycena*. Paris. 710 p.

Lamoure D. 1957a. Amphithallie dans la race bisporique du *Marasmius limosus* Q. Comptes rendus de l'Académie des Sciences 244: 2643–2645.

Lamoure D. 1957b. Hétérocaryose chez les basidiomycétes amphitalles. Comptes rendus de l'Académie des Sciences 244: 2841–2843.

Lamoure D. 1959. L'hétérocaryone des diplontes d'origine monosporique d'un basidiomycète amphithalle démontrée par le "phénomène de Buller." Comptes rendus de l'Académie des Sciences 248: 3479–3480.

Lamoure D. 1960. Recherches cytologiques et expérimentales sur l'amphithallie et la parthénogénèse chez les *Agaricales*. Evolution nucléaire dans la baside des forms bisporique. Thesis. Lyon.

Maerz AJ, Paul MR 1950 A dictionary of color. McGraw Hill, NY.

Mata JL, Hughes KW, Petersen RH. 2004. Phylogenetic placement of *Marasmiellus juniperinus*. Mycoscience 45: 214–221. https://doi.org/10.1007/S10267-004-0170-3

Mata JL, Hughes KW, Petersen RH. 2007. An investigation of /omphalotaceae (*Fungi*: *Euagarics*) with emphasis on the genus *Gymnopus*. Sydowia 58: 191–289.

Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo J-M, Ge Z-W & al. 2006. Major clades of *Agaricales*: a multilocus phylogenetic overview. Mycologia 98: 982–995. https://doi.org/10.3852/mycologia.98.6.982

Miyamoto T, Igarashi T, Takahashi K. 2000. Lignin degrading ability of litter-decomposing basidiomycetes from *Picea* forests of Hokkaido. Mycoscience 41: 105–110. https://doi.org/10. 1007/BF02464317

Moncalvo J-M, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R. 2000. Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. Systematic Biology 49: 278–305. https://doi.org/10.1093/sysbio/49.2.278

Moncalvo J-M, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime MC & al. 2002. One hundred and seventeen clades of euagarics. Molecular Phylogenetics and Evolution 23: 357–400. https://doi.org/10.1016/S1055-7903(02)00027-1

Munsell AH 1961 A color notation. 11th Ed. Munsell Color Co., Baltimore, MD.

Murrill WA. 1915. *Polymarasmius*. North American Flora 9: 286–287.

Mycoportal. 2018. Mycoportal.org/portal/index.php (Accessed 2020).

Oliveira JJS, Ruby V-I, Cabra TS, Rodrigues DP, Ishikawa NK. 2019. Progress on the phylogeny of the *Omphalotaceae: Gymnopus* s. str., *Marasmiellus* s. str., *Paragymnopus* gen. nov. and *Pusillomyces* gen. nov. Mycological Progress. 18: 712–739. https://doi.org/10.1007/s11557-019-01483-5.

Osono T. 2015. Effects of litter type, origin of isolate, and temperature on decomposition of leaf litter by macrofungi. Journal of Forestry Research 20: 77–84. https://doi.org/10.1007/s10310-014-0462-1

Owings PR. 1997. Evolutionary relationships within the genus *Marasmius* inferred by morphological and nrDNA sequence comparisons. Thesis. San Francisco, CA: San Francisco State University.

Owings PR, Desjardin DE. 1997. A molecular phylogeny of *Marasmius* and selected segregate genera. Inoculum 48: Abstracts 28–29.

Peck CH. 1873. Descriptions of new species of fungi. Bulletin of the Buffalo Society Natural Science 1: 41–72.

Peck CH. 1874. Report of the botanist. Annual Report of the New York State Museum 26: 35–91.

Pegler DN. 1965. Studies on Australian agarics. Australian Journal of Botany 13: 323–356. https://doi.org/10.1071/BT9650323

Pegler DN. 1977. A preliminary agaric flora of East Africa. Kew Bulletin Additional Series 6. 615 p.

Persoon CH. 1801. Synopsis methodica fungorum. Gottingiae.

Petersen RH. 1978. Notes on clavarioid fungi. XVI. Clampless taxa in *Clavulinopsis*. Mycotaxon 6: 503–507.

Petersen RH. 1995. There's more to a mushroom than meets the eye: Mating studies in the *Agaricales*. Mycologia 87: 1–17. https://doi.org/10.1080/00275514.1995.12026496

Petersen RH, Hughes KW. 2010. The *Xerula*/*Oudemansiella* complex. Nova Hedwigia Beihefte 137. 625 p.

Petersen RH, Hughes KW. 2016. *Micromphale* sect. *Perforantia* (*Agaricales*, *Basidiomycetes*); Expansion and phylogenetic placement. MycoKeys 18: 1–122. https://doi.org/10.3897/mycokeys.18.10007

Petersen RH, Hughes KW. 2017a. Corrigenda for: "*Micromphale* sect. *Perforantia* (*Agaricales*, *Basidiomycetes*); expansion and phylogenetic placement" published in MycoKeys [10.3897/mycokeys.18.10007] MycoKeys 19: 45–54. https://doi.org/10.3897/mycokeys.19.11565

Petersen RH, Hughes KW. 2017b. An investigation on *Mycetinis* (*Euagarics*, *Basidiomycota*). Mycokeys 24: 1–138. https://doi.org/10.3897/mycokeys.24.12846

Petersen RH, Hughes KW. 2019. Two additional species of *Gymnopus* (*Euagarics*; *Basidiomycotina*). Mycokeys 45: 124. https://doi.org/10.3897/mycokeys.45.29350

Redhead SA. 1980. *Marasmiellus filopes*. Fungi Canadenses 179. 1–2. Agriculture Canada Ottawa.

Redhead SA. 1984. Mycological observations, 412: on *Kuehneromyces*, *Stropharia*, *Marasmius*, *Mycena*, *Geopetalum*, *Omphalopsis*, *Phaeomarasmius*, *Naucoria* and *Prunulus*. Sydowia 37: 246–270.

Restivo JH, Petersen RH. 1976. Studies on nuclear division and behavior within basidia . I. *Hydnum umbilicatum*. Mycologia 68: 666672. https://doi.org/10.1080/00275514.1976.12019951

Retnowati A. 2018. The species of *Marasmiellus* (*Agaricales*: *Omphalotaceae*) from Java and Bali. Gardens Bulletin, Singapore 70: 191–258. https://doi.org/10.26492/gbs70(1).2018-17

Ridgway R. 1912. Color standards and color nomenclature. Publ. Priv., Washington, DC.

Sandoval-Leiva PA, McDonald JV, Thorn RG. 2016. *Gymnopanella nothofagi,* a new genus and species of gymnopoid fungi (*Omphalotaceae*) from Chilean *Nothofagus* forests. Mycologia 108: 820827. https://doi.org/10.3852/15-303

Stevenson G. 1964. The *Agaricales* of New Zealand V. *Tricholomataceae*. Kew Bulletin 19: 159. https://doi.org/10.2307/4108283

Vizzini A, Antonín V, Sesli E, Contu M. 2015. *Gymnopus trabzonensis* spec. nov. (*Omphalotaceae*) and *Tricholoma virgatum* var. *fulvoumbonatum* var. nov. (*Tricholomataceae*), two new white-spored agarics from Turkey. Phytotaxa 226: 119–130. https://doi.org/10.11646/phytotaxa.226.2.2

Wilson AW, Desjardin DE. 2005. Phylogenetic relationships in the gymnopoid and marasmioid fungi (*Basidiomycetes*. *Euagarics* clade). Mycologia 97: 667-679. https://doi.org/10.1080/15572536.2006.11832797